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Molluscan Research

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Growth and development of the rare land snail *Paryphanta busbyi watti* (Eupulmonata : Rhytididae)

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Abstract

The rare carnivorous land snail *Paryphanta busbyi watti* was investigated by following marked snails over a study period of 6.3 years. Large snails were fitted with harmonic radar transponders to aid in locating them. This species is iteroparous and has determinate growth. Shells had maximum diameters of 49.6–61.2 mm. Two to eight large eggs, representing 5%–23% of the live weight of a snail, were laid at a rate of one to two per day over 2–5 days. These eggs were deposited in one to three holes dug in soil by the snails. A newly laid egg was surrounded by an adhesive membrane, which disappeared after a few days, exposing the calcareous shell. The eggs took 5–7.3 months to hatch and the young snails remained underground for a minimum of up to 2.8 months. The shells of these snails increased in size while underground. A non-linear mixed-effects model was used to combine data from 31 snails that were monitored for different lengths of time. Only an approximate estimate could be made of the development rate for young snails. Growth to the adult shell stage was estimated to take 3–4.3 years and fast-developing individuals tended to become larger adults. The maximum time that a snail with an adult shell was monitored was 4.1 years, whereas most snails with an adult shell were monitored for 1–2 years.

Additional keywords: egg incubation, landsnail, lifespan, Pulmonata.

Introduction

Paryphanta busbyi watti Powell, 1946 (Rhytididae) occurs only on the end of the Aupouri Peninsula, Northland, New Zealand (Fig. 1). It is a rare snail that is listed as a highest-priority species for conservation action by the Department of Conservation (Molloy *et al.* 1994). One other subspecies, namely *P. b. busbyi* (Gray, 1840), is widespread from Kaitaia to Warkworth in the upper part of Northland, where it occurs in forest and scrub. Both subspecies are large snails (up to 62 and 79 mm maximum shell diameter, respectively) that feed on earthworms and possibly other ground-living invertebrates (Powell 1979). Both subspecies are fully protected (Wildlife Act (New Zealand) 1953).

Information on *P. b. watti* is limited to its taxonomy (literature included in Powell 1979), distribution (Parrish 1992; Goulstone *et al.* 1993; Sherley 1993) and a description of one egg (Powell 1946). There is more information on the biology and egg of *P. b. busbyi*, but even this is, for the most part, sketchy (Hutton 1881; Powell 1930; O'Connor 1945; Ohms 1948; Dell 1955; Vause 1977; Ballance 1986; Meads 1990; Parrish *et al.* 1995; Montefiore 1996; Coad 1998).

The following research was started while working on the distribution and habitat of *P. b. watti* from 1994 to 1997 (Stringer and Montefiore 2000) and was completed in November 2000. The intention was to provide conservation managers with information on the incubation time, growth rates and longevity to help them make informed decisions relating to the species. For example, it is necessary to have data on the life history

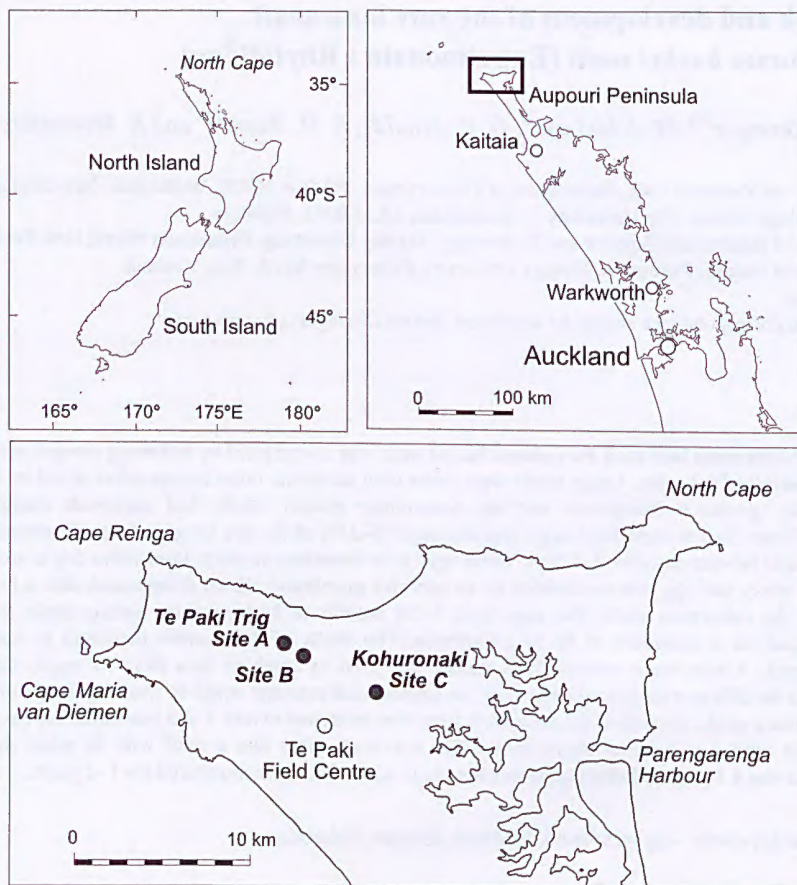


Fig. 1. Map of the North Island of New Zealand, showing the location of *Paryphanta busbyi wattii*.

characteristics of *P. b. wattii* to determine whether these rare snails are likely to become extinct and, if so, how to circumvent this. Information on the distribution, habitat, size-frequency distribution and observed mortality of *P. b. wattii* are given in Stringer and Montefiore (2000), together with some preliminary information on the egg, the time of year when mating and egg laying occur and estimates of rates of movement and of site fidelity for large individuals. More detailed information on some of the latter aspects, together with some data on the age at first and subsequent reproduction and on movements will be published elsewhere.

Paryphanta b. wattii became rare when humans reduced its habitat to a few remnants of original forest at the end of the Aupouri Peninsula during the past 1000 years or so (Gardner and Bartlett 1980; Millener 1981; Goulstone *et al.* 1993; Brook 1999, 2000). During a recent survey, 45 live *P. b. wattii* were found by searching through 13 954 m² of leaf litter in likely habitat (Stringer and Montefiore 2000). Introduced mammals, particularly feral pigs (*Sus scrofa*), prey on these snails. However, the vegetation where *P. b. wattii* still occurs in Te Paki Farm Park has been slowly recovering since it was protected in 1966 and at least one population of snails now appears to be expanding into an area where pig numbers are reduced by frequent hunting (Stringer and Montefiore 2000).

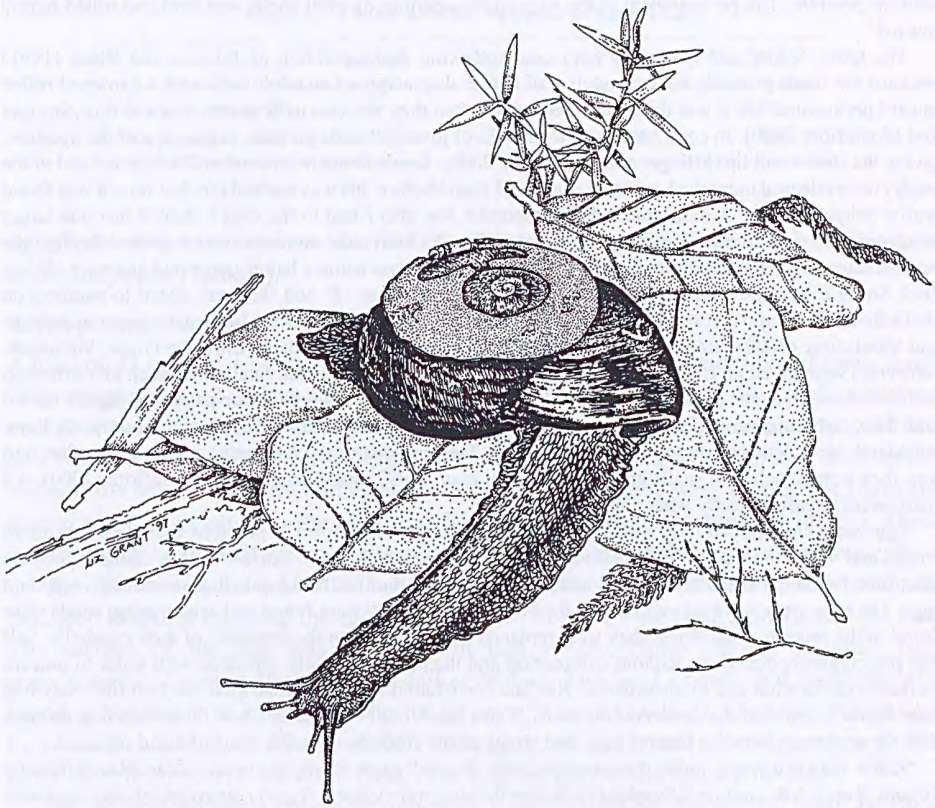


Fig. 2. Diagram of *Paryphanta busbyi watti* with a harmonic radar transponder attached to its shell. The transponder is a C-shaped copper disc with a Z3040 diode (visible at the rear) joining the ends to form a loop. Note the identification number 6 engraved through the periostracum of the shell. (Illustration by E. A. Grant for the cover of *New Zealand Journal of Ecology* 21(2) (1997). With permission from the New Zealand Ecological Society.)

Materials and methods

Because *P. b. watti* is a protected species, special care was taken to ensure that no eggs or snails were harmed. Three sites in Te Paki Farm Park (Fig. 1) were chosen for the present study after a preliminary survey of the area (Stringer and Montefiore 2000). The snails occurred in relatively high densities ($>100 \text{ ha}^{-1}$) in these sites and our activities were limited to areas of less than 2000 m^2 within each site so as to restrict any potential damage to the habitat. Sites A and B were on a ridge running off Te Paki hill and site C was on Kohuronaki Hill (Fig. 1). The exact positions are held by the New Zealand Department of Conservation to protect the snails from shell collectors. Meads *et al.* (1984) have outlined the effects that collectors have had on species of *Powelliphanta* (Rhytididae) in New Zealand.

Twenty six visits were made to the sites between August 1994 and November 2000. Three to six trips were made in January/February, April, June/July, August/September, October and November/December to ensure that samples were taken in all seasons.

Many of the snails were found the first time by searching marked quadrants that were established in each of the three study sites for other purposes (Stringer and Montefiore 2000). These were searched in October/November in most years by sorting through all the litter. Other snails were found for the first time up to 20 m away from these quadrants while searching for snails with harmonic radar transponders attached to them, as described below. Each time a snail was found, the maximum diameter of its shell was taken (Meads *et al.* 1984; Stringer and Montefiore 2000) and a note was made whether the shell was

adult or juvenile. The periostracum at the edge of the aperture of adult shells was hard and rolled tightly inward.

The terms 'adult' and 'juvenile' were used following the convention of Johnson and Black (1991) because the snails probably became adult well before they acquired an adult shell with a hardened rolled inward peristome, but it was difficult to recognise when they were sexually mature prior to this (Stringer and Montefiore 2000). In contrast, the periostracum of juvenile snails projects at the edge of the aperture, giving the shell a soft lip (Stringer and Montefiore 2000). Snails found in November 2000 (at the end of the study) were released unmarked, whereas each snail found before this was marked the first time it was found with a unique number. A harmonic radar transponder was also fitted to the snail's shell if this was larger than approximately 20 mm in maximum diameter (Fig. 2). Individual numbers were engraved through the periostracum of shells greater than approximately 20 mm across using a battery operated engraver (Arlec; Dick Smith Electronics, Wellington, New Zealand). The prefixes 'T' and 'K' were added to numbers on shells from sites A and C respectively. The positions where these numbers were located are given in Stringer and Montefiore (2000). Small numbered labels used for marking queen bees (Christian Graze, Weinstadt, Germany) were glued on if the shells were smaller than 20 mm in diameter. Snails with such identification numbers were given the prefix 'red' below. Each shell was first dried with tissue paper and lightly buffed with fine carborundum paper, then the queen bee label was embedded in clear 5-min Araldite (Selleys, Auckland, New Zealand) on top of the protoconch. Descriptions of the harmonic radar transponders and how they were attached to snails are given in Lövei *et al.* (1997) and Stringer and Montefiore (2000). All snails were released exactly where they were found.

Eggs were cleaned carefully with tissue paper to remove as much soil as possible, then their maximum length and width was taken with callipers. Eggs were weighed to the nearest 0.01 g using a portable electronic balance. Particular care was taken not to damage the fine membrane that surrounds newly laid eggs. The eggs were replaced carefully in the holes in which they were found and, when young snails were found in the process of hatching, they were replaced carefully next to the remnants of their eggshells. Soil was placed gently over them without compaction and the area was lightly sprinkled with water to prevent increased desiccation due to disturbance. Half the nests found were left alone after the first time they had been found because of the conservation status of this snail, but every second nest found was dug up each time the area was visited so that the eggs and young snails could be counted, measured and replaced.

Snails with harmonic radar transponders were located again using harmonic radar (Recco Rescue System; Recco AB, Lidingö, Sweden) each time the sites were visited. A grid pattern search was used with passes 3–5 m apart. This heightened the probability that each snail with a transponder in the search area was found (Lövei *et al.* 1997). The use of harmonic radar enabled us to quickly find any snail with a transponder and to narrow down its position to approximately 0.25 m² of forest floor. This reduced both the amount of hand searching required to find the snails and the disturbance to leaf litter.

The numbers of snails found at each study site during each field trip were too low to analyse separately, so data from all three sites were combined. All means are given with the SEM. The growth of snails with shells 25 mm or more in maximum diameter was described by a non-linear mixed-effects model fitted using S-Plus 5.1 (Mathsoft, Seattle, USA) for Unix.

Results

Overall, 126 live *P. b. watti* snails were found at the three study sites between August 1994 and November 1999. This includes 51 snails that were juveniles when first found and 13 snails that hatched from eggs (Table 1). Queen bee labels were attached to 33 juveniles and harmonic radar transponders were attached to 31 juveniles and 62 adults. There was no

Table 1. Maximum length (mm) of adult shells of snails fitted with harmonic radar transponders at three study sites in Te Paki Farm Park

| Location | Maximum length of adult shells (mm) | | | |
|----------|-------------------------------------|-----------|-----------|-----------|
| | Site A | Site B | Site C | All sites |
| Mean | 56.10 | 56.84 | 56.42 | 56.51 |
| SEM | 0.69 | 0.45 | 0.75 | 0.34 |
| Range | 49.6–60.8 | 53.0–60.5 | 50.4–61.8 | 49.6–61.8 |
| <i>n</i> | 16 | 24 | 12 | 52 |

Table 2. Clutch size for *Paryphanta bushyi watti*

| | Median | Range | Mean | SEM |
|--------------------|--------|-------|------|------|
| No. eggs per nest | 2 | 1-8 | 3.42 | 0.70 |
| No. eggs per snail | 5 | 2-8 | 5.40 | 1.03 |

significant difference between the maximum diameters of shells from adult snails at the three study sites (Table 1).

Development of the egg

A total of 41 eggs in 13 clutches produced by eight snails was found. Five of these snails were monitored for 2–5 days and laid an average of 5.4 eggs (Table 2). Two snails remained over their holes for 2–3 days and laid one to two eggs per night, whereas another snail laid one, two and two eggs in three different holes over 4 days. Data on clutch size are minimal because the snails may have laid eggs in other nests before they were found. The mass and size of snails in relation to the eggs they laid are given for three snails in Table 3. These were the only snails that were weighed on consecutive days while they were laying eggs.

One egg was found just after laying by snail T11. The front half of this snail was extended from the shell and the egg was partly enveloped by the ventral surface of the foot. The surface of the egg was smooth, but had a honeycomb pattern of white cells approximately 2 mm in diameter with darker centres. Another 17 newly laid eggs were also found either singly or among clutches of up to eight eggs (Table 2). Each was surrounded by a smooth and slightly adhesive tough white layer, which formed a loose membrane. This outer layer disappeared after 1–2 days, exposing the hard white calcareous shell.

The incubation time is known for only three eggs from different clutches (Table 4). These eggs were found just after they had been laid and the juvenile snails were subsequently found while they were in the process of hatching. Eggshells of mature eggs had a mosaic of fine cracks and broke apart as soon as they were touched. Two of these eggs were found when newly laid beneath snails with transponders and another was found during a casual search for snails approximately 40 m from site B. The eggs hatched 152, 213 and 221 days after being laid on 7 February 1995, 3 February 1996 and 8 April 1996 respectively (Table 4).

There is an indication that eggs may lose weight as they develop and that the rate of weight loss increases as incubation progresses (Fig. 3). However, individual eggs were not marked, so this could not be tested statistically. The mass of one egg that was monitored remained approximately constant during incubation, whereas five other eggs lost weight. Two of the

Table 3. Relationship between the dimensions of the snails (weighed after ovipositing) and the eggs they laid

| Snail no. | Max. length snail (mm) | No. eggs measured | Max. length of eggs (mm) | Mass of eggs (g) | Mass of snail after laying (g) | Notes |
|-----------|------------------------|-------------------|--------------------------|------------------|--------------------------------|---|
| 20 | 60.18 | 1 | — | 1.01 | 43.5 | Laid seven eggs (total 7.61 g) on 1 November 1997 |
| K4 | 59.38 | 1 | 12.62 | 0.93 | 29.98 | Laid two eggs by July 1997; second egg was not weighed |
| T25 | 56.18 | 5 | 14.54–14.99 | 6.26 | 28.52 | Snail was 30.8 g after laying three eggs (3 eggs 3.90 g). |

Table 4. Incubation period for eggs and the time spent by newly hatched snails underground in their nests

| | | <i>n</i> | Duration (days) | | | |
|----------------------|-------------------------|----------|-----------------|-------|--------|---------|
| | | | Mean | SEM | Median | Range |
| Eggs that died | Maximum time alive | 4 | 135.3 | 18.7 | 149 | 81–163 |
| Eggs that hatched | Known incubation time* | 3 | 195.0 | 21.6 | 213 | 152–221 |
| | Maximum incubation time | 14 | 204.2 | 6.8 | 202 | 140–229 |
| Snails that died | Maximum time alive | 4 | 59.8 | 19.3 | 79 | 2–79 |
| Snails that survived | Minimum time in nest | 15 | 12.1 | 7.0 | 0 | 0–85 |
| | Maximum time in nest | 15 | 95.5 | 19.96 | 62 | 0–200 |

*Incubation times for eggs from an unmarked snail and from snails 3 and K4.

latter eggs subsequently died. Individual eggs were unable to be identified in the remaining three clutches of five to eight eggs, even though maximum lengths and widths were measured (Fig. 3). These measurements were difficult to take accurately because of the risk of damaging the fragile shell with the callipers. Overall, 82.8% of eggs hatched successfully and, of those that died, one was crushed by cattle and the remaining four died for unknown reasons.

Growth

Only fragmented data were obtained on the growth rate of *P. b. watti* and on the length of time that adults live. After hatching, the snails remained underground in their nests on average for a minimum of 12 days and a maximum of 95 days (Table 4). However, 12 snails were never seen alive because their nests were checked after they had left, so this minimum period is conservative. The minimum periods that the three snails were seen alive in their

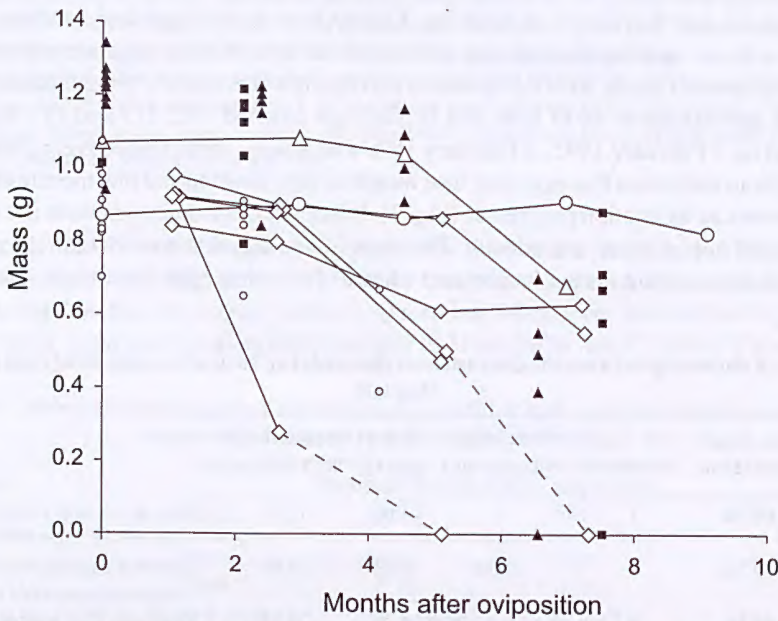


Fig. 3. Changes in the mass of the eggs during incubation. Symbols indicate eggs in the same clutch.

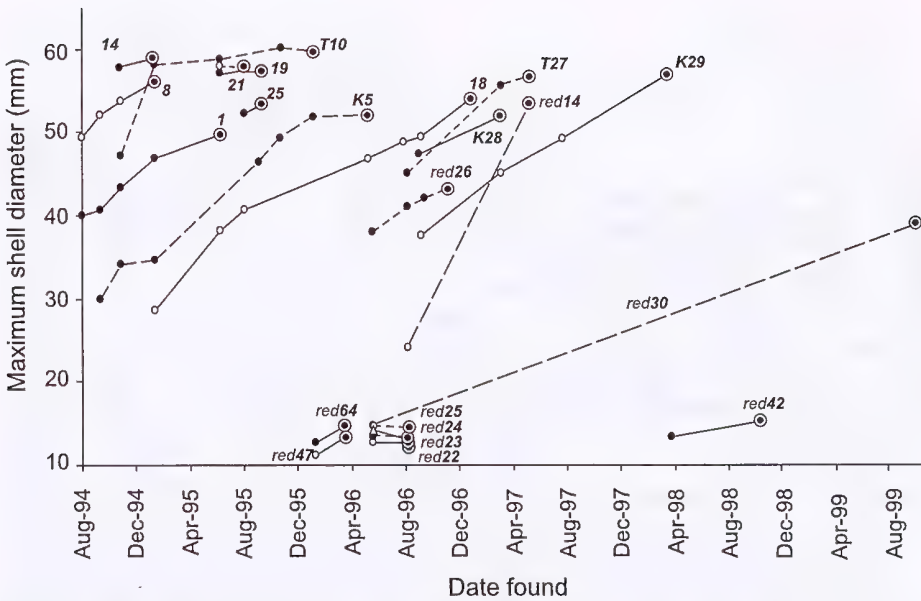


Fig. 4. Growth of juvenile *Paryphanta busbyi wattii*. Data are for snails that did not develop adult shells during the study. Labels are identification numbers of snails.

nests were 32, 65 and 85 days. None of the six snails that hatched within the study sites and survived was found again after leaving the nest.

The shells of young snails in nests were difficult to measure because the edge of the aperture was very delicate and flexible. However, the shells of all six snails that were measured in the study sites grew because their apertures extended beyond a slight deformity that marked the edge of the protoconch at hatching. Five of these snails died while underground; however, the shell of one had clearly increased in size, whereas three other shells were approximately the same size and the last shell had, apparently, become smaller. The shell of the snail that survived (red-47) clearly increased in diameter (Fig. 4) and increased in mass from 0.39 to 0.47 g.

Juvenile snails that had left the nest grew at widely differing rates, although they tended to slow down as they approached adult size (Figs 4,5). Only one snail (red-30) was recaptured after being first found with a shell slightly larger than a newly hatched snail. This snail grew from an initial maximum shell diameter of 14.9 mm to 39.1 mm over 1241 days (Fig. 4). Three other snails with initial shell diameters of less than 30 mm and two with shells between 30 and 40 mm in diameter were monitored until they were almost mature. Twenty-four larger juveniles were recaptured at least twice and 13 of these were monitored until they were adults (Figs 4–6). A further 33 juvenile and 28 adult snails were not recaptured.

Estimation of growth rate

The early stages of growth were particularly difficult to estimate because only one snail was recaptured that, when first found, was approximately the size of snails that emerge from nests, one snail was recaptured that was initially one-third grown and another four snails were recaptured that were initially less than two-thirds grown. Thus, there are not sufficient

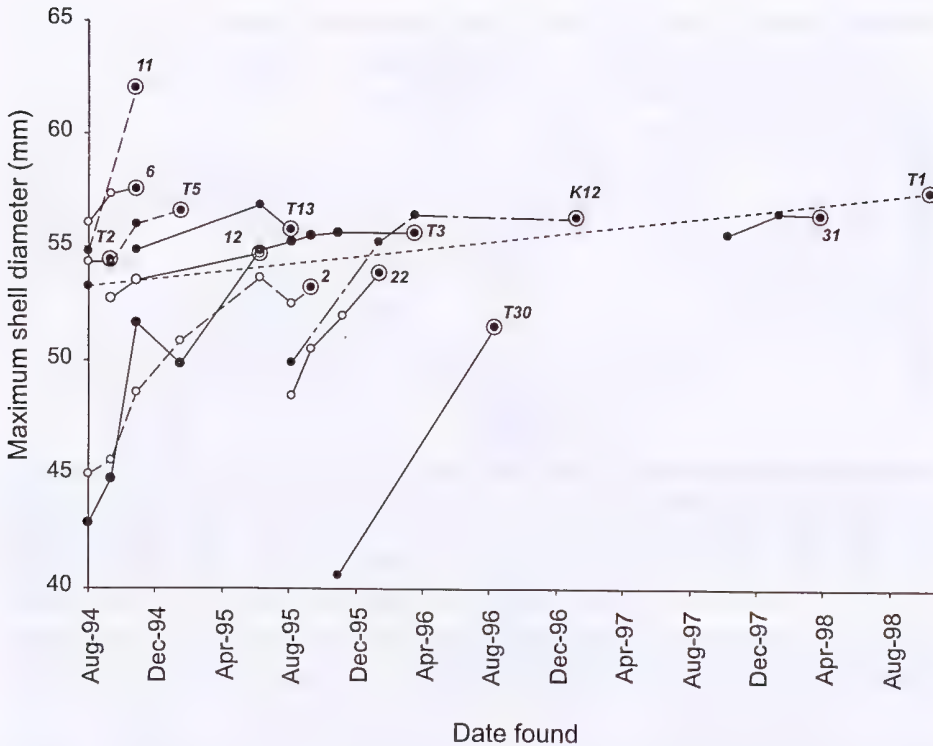


Fig. 5. Growth of snails that developed adult shells. Labels are identification numbers of snails.

data to estimate growth rates reliably for snails until they are approximately three-quarters grown (shells 40–45 mm across). The low recapture rates for small snails resulted because of relying on finding them either by chance encounters or during annual searches of marked quadrants. Only when the snails were large enough to have a harmonic radar transponder attached to their shells were they recaptured more frequently.

Growth through the development period of the juvenile phase (i.e. snails with shells less than 45 mm in maximum diameter) was estimated first. A morphometric change in shell shape occurs at approximately 45 mm in *P. b. watti* (Stringer and Montefiore 2000), which is usually associated with reproductive organ development in other pulmonates and is indicative of a change from juvenile to adult growth (e.g. Williamson 1976; Solem and Christensen 1984; Lazaridou-Dimitriadou 1995). In addition, there is also evidence that the growth rate of juvenile snails may differ from that of adults in some species (e.g. Baur 1989; Lazaridou-Dimitriadou 1995).

Two different methods were used to estimate growth rate. First, the minimum and maximum times to reach a shell size of 45 mm were estimated by adding together the growth curves of each snail, starting with the smallest (red-30) and adding the others in order of their initial size. The growth curve for each snail was started at the point where its size corresponded with the estimated sizes of the respective growth curves of the fastest and slowest snails previously added (Fig. 7). This method gave a minimum of 674 days and a maximum of 1107 days to reach 45 mm. The average developmental time was then estimated by averaging the developmental times of both growth sets (fastest and slowest

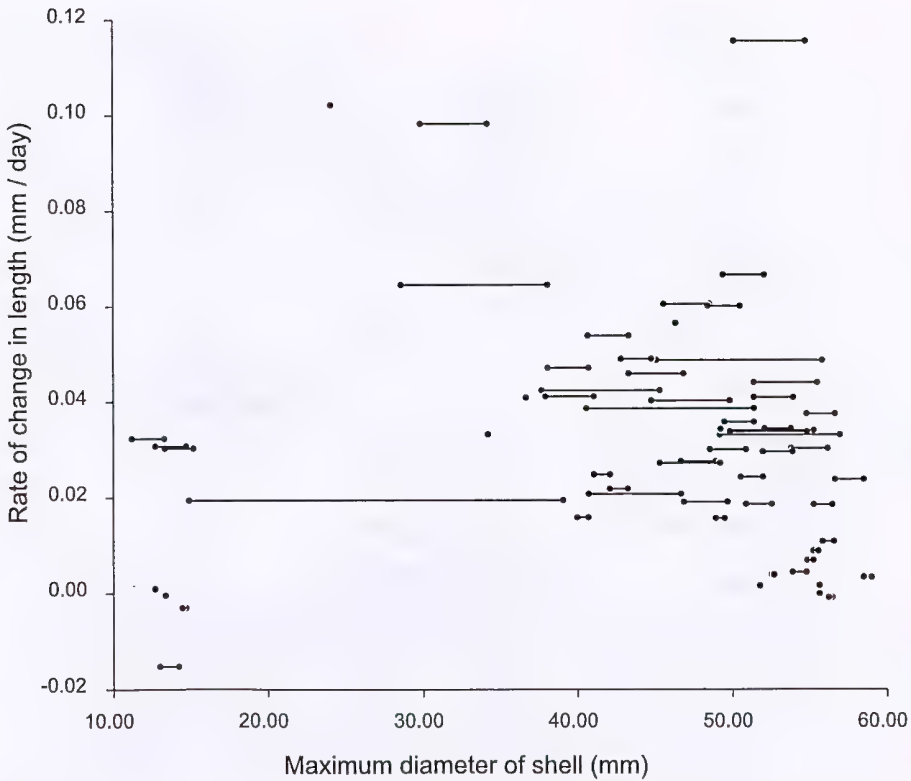


Fig. 6. Growth rates of snails. The daily rate of change in maximum shell diameter is shown in relation to the increase in shell size between recaptures for all snails shown in Figs 3 and 4.

growth patterns). This gave an average time of approximately 910 days to reach a shell diameter of 45 mm (Fig. 8).

The second method was to add the growth pattern of each successively larger snail to the others at the point where its initial size corresponded with the average time taken for all smaller snails to reach this size. For example, the growth patterns of the two smallest snails were added together, as shown in Fig. 7, then the average time was estimated for these to reach the initial size of the third-largest snail. The growth pattern for the latter was then added at this point and the process was repeated for subsequent snails. This method gave an estimated average time of 937 days for snails to reach a shell size of 45 mm (Fig. 8).

Neither of these two methods makes any assumptions about the shape of the growth curve. Figure 6 suggests that, although there is considerable variability, for maximum diameters of approximately 30 mm and above the growth rate decreases with increasing maximum shell diameter, which implies a curve that approaches an asymptote exponentially as described below:

Maximum length l of shell i at time t after marking = $A_i(1 - e^{-B(t+T_i)})$ if the shell has a soft lip at t

or

Maximum length l of shell i at time t after marking = A_i if the shell has a hard lip

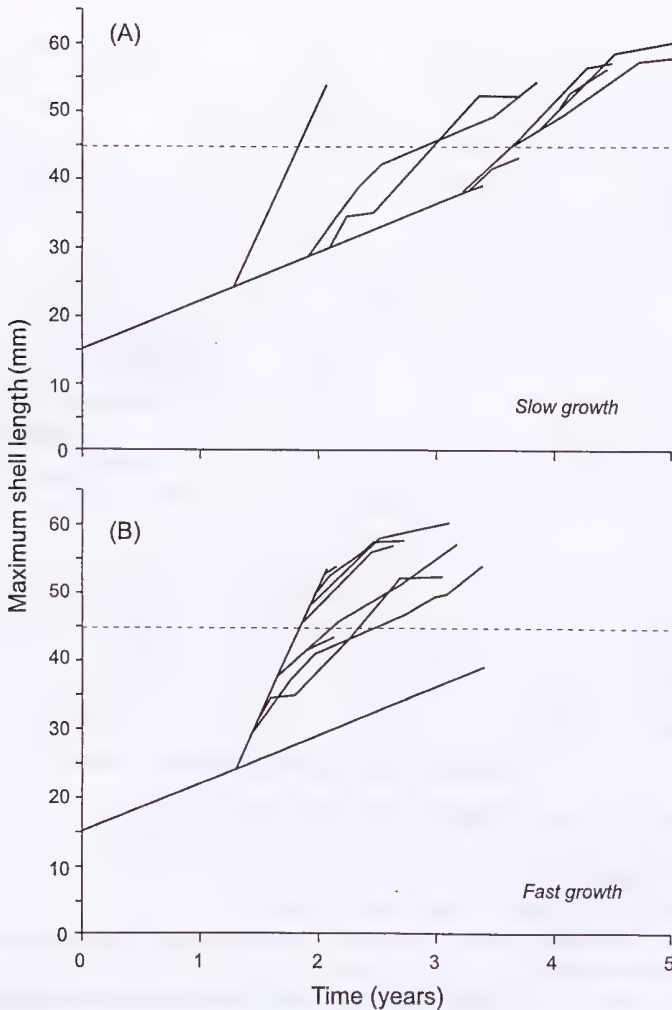


Fig. 7. Growth patterns of *Paryphanta busbyi wattii* up to a maximum shell diameter of 45 mm. The growth pattern of each successively larger snail was added at the point where its initial size corresponds to the estimated size that an initially smaller snail had grown to in order to provide (a) the fastest overall growth rate and (b) the slowest overall growth rate.

where A_i is the ultimate diameter of the i^{th} shell, (estimated mean (\pm SEM) 55.8 ± 1.2 mm; estimated standard deviation 3.4 mm) and the mean of A_i is the mean maximum diameter of adult shells, B is the growth rate, assumed constant for all snails, of 0.0051 ± 0.0006 and T_i is an adjustment for the age of the i^{th} snail when first marked (estimated mean (\pm SEM) 318 ± 48 days).

The snails found were assumed to be a random sample from a population of snails over which A_i and T_i vary. The parameter T_i , using a non-linear mixed-effects model, slides the growth curve horizontally for an individual snail to fit the overall curve, thereby aligning the curves for different snails on the one plot (Fig. 9). In practice, this

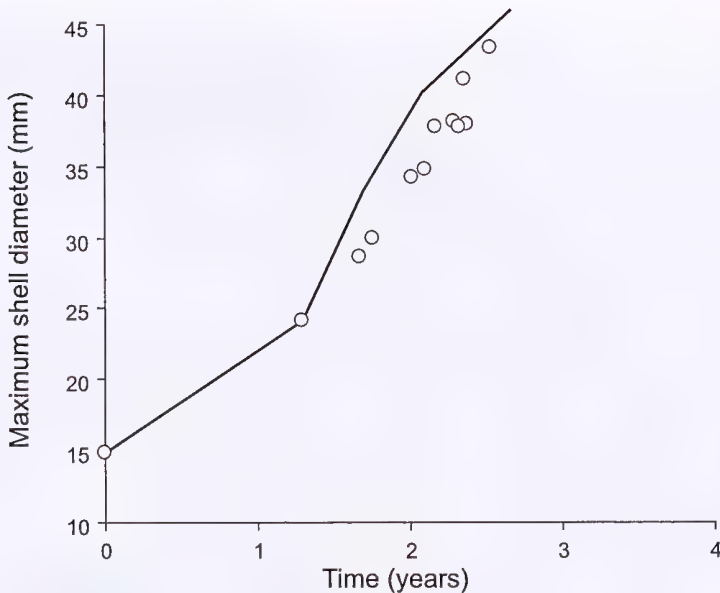


Fig. 8. Average developmental growth patterns of *Paryphanta busbyi wattii* up to a maximum shell diameter of 45 mm. The open circles indicate average developmental times from Fig. 7A,B combined; the solid line indicates average developmental times of snails when the developmental pattern of each successively larger snail was started off at the average time taken for all other snails to reach its initial size.

means that snails with only a few points can be made to fit any curve and five points were needed per snail to enable the model to be fitted. Note that $T=0$ does not correspond to any particular stage of snail development because the model will not fit earlier growth.

On average, snails 45 mm across took a further 430 days before they acquired adult shells (at Day 746 on the graph in Fig. 9). Overall, the average time taken for *P. b. wattii* snails to develop full adult shells was estimated as 3.7 years and they could conceivably grow to this stage anywhere between approximately 3.0 and 4.3 years. This is an estimate of the maximum developmental period because it is based on the times when the shell of each snail was first observed to have a hard aperture lip. The minimal developmental period (the time when each snail was last observed with a soft-lipped shell) is, on average, 0.61 ± 0.26 years (median 0.36 years) earlier than this.

Lifespan of the adult

Ten juvenile snails developed adult shells. Four were subsequently found dead and the others were recaptured at least once before they moved out of the search areas. The periods when the snails were known to be alive are given in Table 5. Another 39 snails were first found with adult shells. Fourteen of these died, another 23 were recaptured at least once before they moved out of the search areas and two were found alive during the last search. The periods that they were known to be alive are given in Table 5.

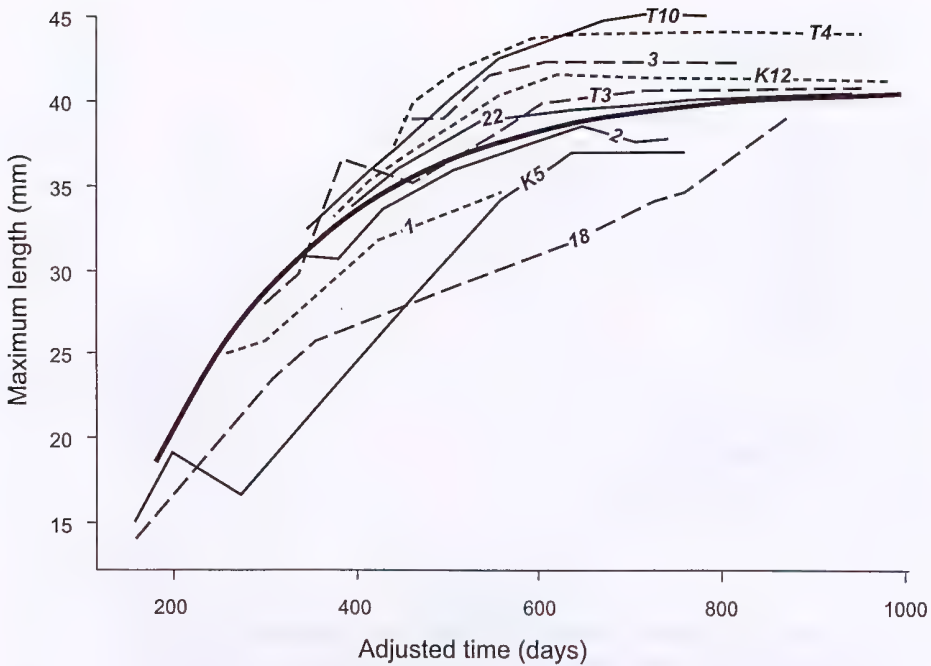


Fig. 9. A non-linear mixed-effects growth model (see text for details) fitted to data for snails that were found five or more times. The thicker curved line shows the growth of an average snail and the lines around it are growth curves for individual snails. Labels are identification numbers of snails.

Discussion

The life history of *P. b. watti* has been sketched out from a series of observations of portions of individual life histories taken from many different snails. This is partly because the snails are both relatively long lived and develop slowly in relation to the time span of our study and partly because of the low numbers of these rare snails that were monitored.

Table 5. Observed life expectancy of adult snails

The minimum period is the time taken from when snails were last seen alive and the maximum period is taken to when they were found dead

| Category of adult snail | n | Minimum period (years) | | | Maximum period (years) | | |
|---|----|------------------------|--------|-----------|------------------------|--------|-----------|
| | | Mean \pm SEM | Median | Range | Mean \pm SEM | Median | Range |
| Found as juvenile, died as adult | 4 | 0.65 \pm 0.38 | 0.60 | 0–1.42 | 1.13 \pm 0.23 | 1.19 | 0.53–1.59 |
| Found as adult and died | 12 | 1.24 \pm 0.26 | 1.04 | 0–2.35 | 1.84 \pm 0.32 | 1.71 | 0.26–3.18 |
| Found as juvenile, lost as adult | 6 | 0.56 \pm 0.47 | 0.58 | 0.38–2.75 | – | – | – |
| Found as adult, moved out of area | 27 | 1.07 \pm 0.19 | 0.49 | 0.18–3.19 | – | – | – |
| Found as adult and alive on last search | 2 | 1.97 | – | 1.55–2.40 | – | – | – |

Egg development

The incubation period of between 5.5 and 7.5 months for the eggs of *P. b. watti* is close to the 5 months or more reported by Coad (1998) for three eggs of *P. b. busbyi*. These incubation periods are long in relation to most pulmonates that do not have egg dormancy, but they are similar to those of species of *Powelliphanta*, which take 2–6 months (K. J. Walker, personal communication). Species of *Wainuia* (Rhytididae) are much smaller than *Paryphanta* or *Powelliphanta* and take approximately 2 months to hatch (Meads 1990).

Much of the apparent variability in incubation periods for the eggs of *P. b. watti* is due to the long periods between monitoring them. Even the incubation periods for the three eggs that were found in the process of hatching are probably approximate because it appears that these snails hatch gradually as the eggshells progressively crack and break up towards the end of incubation. It is also likely that these snails were released prematurely because the eggshells broke up as they were examined. However, all three snails subsequently survived. Some of the variability in incubation times may be due to differences in the temperatures that the eggs experienced during incubation. Thus, of the three eggs that were observed in the process of hatching, one laid in February (summer) had an incubation period that was 66%–71% as long as the incubation period for eggs laid in July and August. However, our sampling intervals were too far apart to demonstrate this effect with other eggs.

Both O'Connor (1945) and Powell (1979) reported that eggs laid by species of *Powelliphanta* have a glossy membranous 'cuticle' that is a pale buff colour, but they did not observe this in either *Paryphanta busbyi busbyi* and other rhytidid genera. Newly laid eggs of *P. b. watti* do possess such a membrane, although it is white, but it subsequently disappears within a few days to expose the hard calcareous eggshell.

The shells of adult snails account for 19.0%–19.2% of the total mass of the snails (Stringer and Montefiore 2000); therefore, the individual eggs laid by snails 20 and K4 represent 2.8%–3.1% and 3.7%–4.1% of the live mass of these snails before oviposition, respectively. Snail T25 lost 21.5%–23.3% of its original live mass by laying five eggs (Table 3). The average weight loss during oviposition is estimated as $23.2 \pm 4.5\%$ from the average masses of complete adult snails (31.60 ± 0.50 g), their shells (6.04 ± 0.32 g) and eggs (1.10 ± 0.05 g), together with the average number of eggs laid (Table 2).

Growth period

Newly hatched *P. b. watti* snails remain underground at the nest site after they hatch and the shells of some of these snails clearly grow while they are underground. In contrast, it is doubtful whether the three newly hatched snails of *P. b. busbyi* observed by Coad (1998) remained underground for long because all had left the nest within 9–18 days after the eggs were observed in the process of hatching. It is not known whether newly hatched snails of *P. b. watti* feed while underground, but no evidence of faecal matter was found with the snails. Thus, the 20% gain in mass that one of them experienced while underground may have been due to water uptake, whereas the increase in shell size could have been supported by reserves within the snails themselves.

What is the advantage for young snails of remaining underground? Juveniles of *Helicella pappi* (Schütt, 1962) also remain buried for some time and Lazaridou-Dimitriadou (1995) suggested that it may be safer for them to do so until environmental factors are suitable for their activity. This may be especially appropriate during the harsh winters that *H. pappi* experience in Greece. Moisture seems to be the most important environmental factor for young *P. b. watti* snails, yet the period these snails remained underground seems unrelated to this. Summer at Te Pahi is dry and this is when the area has the lowest number of rain

days (approximate summer monthly averages: 91 mm rain, 8 rain days), whereas winter is the wettest season (164 mm rain, 18 rain days; New Zealand Meteorological Service 1983). However, the period spent underground by young snails seems unrelated to whether they hatched in summer, autumn or spring. Possibly, there is some other protective advantage for young *P. b. watti* remaining underground yet to be discovered.

Stringer and Montefiore (2000) found that no size cohorts were evident among juvenile snails because of the relatively low numbers of snails found and because *P. b. watti* has widely overlapping generations. Therefore, Stringer and Montefiore (2000) were unable to estimate the growth period by following size cohorts, as has been done for other snails (Williamson 1976; Johnson and Black 1991 and references therein). Attempts were not made to estimate growth rates by using annual growth deformities on the shell because these were often hard to recognise and many shells lacked them altogether. This method may also be unreliable, as discussed below. The only data that were collected for estimating the growth period are portions of growth patterns from different snails.

The two methods used to estimate the time for snails to reach a maximum shell size of 45 mm gave similar results. However, one method indicated a gradual decrease in growth rate with increasing size, whereas the other method indicated a gradual increase in growth rate with increasing shell size up to 45 mm. The first pattern appears to correspond with the growth pattern that Coad (1998) found for *P. b. busbyi* at Trounson Park. This is the usual growth pattern for most gastropods (Wilbur and Owen 1964). Coad (1998) reported that the smallest snails (16 mm) had the fastest growth rate and that growth rate progressively decreased with increasing shell size. Coad's (1998) data set ($n = 79$) was larger than the one presented here and included six snails with shells between 16 and 30 mm across and another 27 snails with shells up to 30 mm across. Therefore, Coad's (1998) estimates of overall growth are correspondingly better than ours. Despite this, we believe that the growth rates of small *P. b. watti* may very well be depressed because Te Pahi is drier (lower rainfall, fewer rain days, lower average relative humidity and higher average temperature; New Zealand Meteorological Service 1983) than Trounson Park. Thus, small *P. b. watti* snails would experience fewer nights that were moist enough for them to be active compared with young *P. b. busbyi*. Another possible indication that the environment at Te Pahi is harsher than at Trounson Park is that young *P. b. watti* experience a much higher mortality rate than young *P. b. busbyi* at Trounson Park (Stringer and Montefiore 2000).

Stringer and Montefiore (2000) gave a rough estimate of 2.6–3 years for *P. b. watti* to grow to maturity. However, the three smallest snails they found had shells 24, 29 and 30 mm in diameter, so they had to base their growth estimate on the assumption that snails smaller than this grew at the same rate as the initial growth rate of these three snails. This was justified by Coad's (1998) observation that the growth rate of *P. b. busbyi* was fastest when it was small (shell diameter of 15 mm) and decreased with increasing shell diameter. Coad (1998) estimated that *P. b. busbyi* takes approximately 3 years to grow to the stage where its shell has a hard lip, whereas Dell (1955) estimated that *P. b. busbyi* takes 7 years to reach full adult size from an examination of growth ridges on the shells. Dell (1955) assumed that these ridges were caused by annual dry periods during the summers and estimated that the shells increased in diameter from 4 to 12 mm each year, but this is a low annual increment in relation to Coad's (1998) observed increases of approximately 15–19 mm each year. However, Dell's (1955) collection site was open scrub, where there were probably high temperatures and a lack of moisture during summer. The use of annual growth rings to estimate the age of pulmonates can also be unreliable for a variety of reasons (see Comfort (1957), Oosterhoff (1977) and Williamson (1979) for a discussion),

even though other authors have used this method to estimate pulmonate age (Pollard *et al.* 1976; Oosterhoff 1977).

Overall, the growth rates of *Paryphanta* seem relatively fast in relation to other large rhytidid snails that occur further south in New Zealand. The shells of three *Powelliphanta hochstetteri obscura* (Beutler, 1901) increased in diameter by approximately 1.5 mm per year in captivity (Meads *et al.* 1984) and Devine (1997) found that the shells of marked individuals of *Powelliphanta traversi traversi* (Powell, 1930) increased, on average, by 2.6 mm per year (range 0.5–10.7 mm) in forest near Levin. In contrast, species of *Wainuia* reach adult size in approximately 6–12 months (Meads 1990), although they only grow to maximum shell diameters of 11.5–38 mm (Efford 1998). Compared with pulmonates that live elsewhere in temperate regions, a growth period of 3–4.6 years seems higher than average, but not by any means extreme. Most have annual or biennial life cycles if they do not undergo periods of dormancy. Larger tropical pulmonates may mature within 1–3 years (Comfort 1957; Peake 1978; Mead 1979; Cain 1983; Solem and Christensen 1984). Exceptions include medium-sized camaenids from Puerto Rico and small Hawaiian achatinellids, which take 3–6 and 4–7 years, respectively, to reach adult size (McLauchlan 1951; Heatwole and Heatwole 1978; Hadfield and Mountain 1980; Hadfield 1986).

In pulmonates, a wide variation in the size of shells of mature snails (e.g. Oosterhoff 1977; Vermeij 1980; Kemp and Bertness 1984; Johnson and Black 1991) and in growth rate (e.g. Heatwole and Heatwole 1978) is quite usual. Also, it is not unusual that faster-growing individuals may often become larger adults (Wolda 1970) and this appears to hold for *P. b. watti* (Fig. 9). The growth rates of pulmonates, as well as the final adult size of their shells, can be affected by many environmental factors, but moisture seems to be the most important factor at times when the snails are not in cold-induced dormancy. Lack of moisture, in particular, may reduce growth indirectly by preventing the snails from being active (Potts 1975; Oosterhoff 1977; Solem and Christensen 1984; Goodfriend 1986; Johnson and Black 1991; Lazaridou-Dimitriadou 1995). Differences in growth rate and the resulting changes in adult size could affect both juvenile mortality rate and reproductive rate and, thus, affect population density (Oosterhoff 1977). Therefore, such variations in growth rates may have far-reaching consequences for population dynamics and evolution (Heatwole and Heatwole 1978).

Total lifespan

Adult *P. b. watti* are known to be able to live at least 4.1 years, although the average time all adult snails were monitored (including those that died) was 1.1 ± 0.1 years. When this is added to the average growth period, this gives an average lifespan for *P. b. watti* after hatching of approximately 4.8 years. This estimate is conservative because it includes the lifespans of those snails already adult when first found and the adult periods used are minima (time to last found alive). In contrast, by using the estimated maximum growth period and the maximum known adult period, an individual snail could, conceivably, live for at least 8.8 years. Such a lifespan seems relatively short in comparison with the suggestions proposed by Powell (1946) that there are at least 15 years between generations of *Powelliphanta* and by Meads *et al.* (1984) that larger species of *Powelliphanta* (60–70 mm) may live 40 years or more. In relation to other temperate-zone pulmonates, the lifespan of *P. b. watti* seems to be long, but not extreme, because larger temperate-zone pulmonates usually have a lifespan of several years and some can live 10 years or more (Comfort 1957, Staikou *et al.* 1988; Lazaridou-Dimitriadou 1995).

Overall, *P. b. watti* are large snails that are relatively long lived, are slow developing and probably have a low reproductive rate. Such life history traits are commonly associated with the absence of predatory mammals and are among the features that characterise the New Zealand fauna (Daugherty *et al.* 1993).

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Some Recent Thraciidae, Periplomatidae, Myochamidae, Cuspidariidae and Spheniopsidae (Anomalodesmata) from the New Zealand region and referral of *Thracia reinga* Crozier, 1966 and *Scintillona benthicola* Dell, 1956 to *Tellimya* Brown, 1827 (Montacutidae) (Mollusca : Bivalvia)

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Abstract

Thracia vitrea (Hutton, 1873) is redescribed and referred to *Thracia* Blainville, 1824, subgenus *Odoncineta* O. G. Costa, 1829. The circum-Antarctic species *Thracia meridionalis* E. A. Smith, 1885 is newly recorded from New Zealand and referred to subgenus *Crassithracia* Soot-Ryen, 1941. New thraciids are described belonging to *Asthenothaerus* Carpenter, 1864 (one), *Parvithracia* Finlay, 1926 (*s. str.*) (one), *Parvithracia* (*Pseudoasthenothaerus*) Kamanov, 2002 (two) and *Trigonothracia* Yamamoto & Habe, 1959 (one). *Myadora biconvexa* Powell, 1927 and *Parvithracia cuneata* Powell, 1937 are referred to *Barythaerus*, a new genus of Thraciidae. *Thracia reinga* Crozier, 1966 and *Scintillona benthicola* Dell, 1956 are referred to *Tellimya* Brown, 1827 in Montacutidae. The periplomatid *Pendaloma micans* (Hedley, 1901) is newly recorded as widely distributed off New Zealand. New data on shell morphology and distributions are provided for the myochamids *Hunkydora novozelandica* (Reeve, 1859) and *Myochama tasmanica* (Tenison Woods, 1877) and new species of *Hunkydora* Fleming, 1948 and *Myadoropsis* Habe, 1960 are described. *Cuspidaria aupouria* Dell, 1950 is referred to *Rhinoclama* Dall & E. A. Smith in Dall, 1886 (*s. str.*). A new and minute species of the Cuspidariidae from the Norfolk Ridge is referred to a new genus, namely *Pseudogrippina*, and cuspidariids belonging in *Plectodon* Carpenter, 1864 (three) and *Rhinoclama* (*Austroneaera*) Powell, 1937 (two) are described. The three *Rhinoclama* (*Austroneaera*) species previously recorded from the New Zealand region are reviewed. Spheniopsidae is transferred from Heterodonta to Anomalodesmata and tentatively grouped in Cuspidarioidea. Six new spheniopsids of the genus *Grippina* Dall, 1912 are described and *G. aupouria* (Powell, 1937) is redescribed.

Additional keywords: *Asthenothaerus*, *Austroneaera*, *Barythaerus*, *Crassithracia*, *Grippina*, *Hunkydora*, *Myadoropsis*, *Myochama*, new taxa, *Odoncineta*, *Plectodon*, *Pseudoasthenothaerus*, *Pseudogrippina*, *Rhinoclama*, *Trigonothracia*.

Introduction

The subclass Anomalodesmata is a large group of highly derived marine bivalves characterised by diverse and distinctive anatomies and shells. The gills are modified to form a unique muscular pump in the carnivorous species (Cuspidariidae, Poromyidae and, to some extent, Verticordiidae) or have a reduced and dorsally reflected outer demibranch in the deposit feeders and filter feeders (other families; Prezant 1998 and references therein). The hinge typically lacks teeth, although secondary teeth are present in some taxa. The primary ligament may be internal or external, supplemented in some taxa by a dorsal secondary ligament that helps maintain alignment of the valves. The inner primary ligament is characteristically elongated and calcified as a lithodesma, which is involved with load distribution in the hinge area and alignment and opening of the valves (Yonge and Morton 1980).

The present contribution was initiated during routine identification in preparation for databasing, when I recognised six undescribed *Grippina* species, which almost doubles the number of living Spheniopsidae known from the world. Besides describing these, the

opportunity is taken to disentangle the three distinct species belonging to three genera in two families currently confused under *Hunkydora novozelandica* (Reeve, 1859) and to record additional related species.

Materials and methods

Shells smaller than 10 mm in maximum dimension were selected, soaked in aqueous wetting agent (trisodium phosphate solution), briefly soaked in strong commercial bleach (to remove traces of soft tissue), washed and cleaned ultrasonically in distilled water and stored in 90% ethanol. They were then dried and affixed to aluminium stubs with conductive carbon tape, 'wired' with conductive carbon paint, sputter-coated with carbon and gold-palladium and examined and digitally imaged with a scanning electron microscope. Larger shells were cleaned and photographed uncoated under artificial light with a digital camera. Distribution maps were prepared by downloading personally verified coordinates for personally verified lots from the museum's database (Te Kahui) onto appropriate maps using a commercial mapping program and final plates were prepared using a commercial digital image manipulation program. Shells were measured with a calibrated optical graticule in a stereomicroscope. Shell terminology follows Cox (1969).

Institutional abbreviations and text conventions

| | |
|------|--|
| AIM | Auckland Institute and Museum, Auckland |
| AMS | The Australia Museum, Sydney |
| BMNH | The Natural History Museum, London |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| NMNZ | Museum of New Zealand Te Papa Tongarewa, Wellington |
| NSMT | National Science Museum, Tokyo |
| NZGS | Institute of Geological and Nuclear Sciences, Lower Hutt |
| NZOI | National Institute of Water and Atmospheric Research, Wellington |
| PI | Prodissoconch I |
| PII | Prodissoconch II |
| pr | pair of valves of single individual |
| RRS | Royal Research Ship |
| RV | Research Vessel |
| SS | Sailing Ship |
| v | valve |
| ZMB | Zoological Museum, Humboldt University, Berlin |

Unless specified, all material examined is at NMNZ (registration numbers preceded by 'M.').

In descriptions of ligamental structures, I have used the term 'sunken' for resilifers that have migrated (in an evolutionary sense) from the hinge line to a position behind/beneath the hinge line as viewed from the valve plane. A sunken resilifer (= subumbonal plate of Kamanev 2002) is associated with a secondarily enlarged ligament that may be calcified (= lithodesma of many Anomalodesmata and some Montacutidae).

Systematics

Class **BIVALVIA** Linnaeus, 1758

Subclass **ANOMALODESMATA** Dall, 1890

Superfamily **THRACIOIDEA** Stoliczka, 1870

Family **THRACIIDAE** Stoliczka, 1870

Genus *Thracia* Blainville, 1824

Thracia Blainville, 1824: 347. Type species (by monotypy: two species group taxa originally included, one of which is a *nomen nudum*): *Mya pubescens* Pulteney, 1799; Recent, Europe. For discussion of authorship of *Thracia* and its type species, see Coan (1990a).

Osteodesma Blainville, 1827: 659. Type species (by subsequent designation of Dall, 1903: 1522): *Anatina myalis* Lamarck, 1818 = *M. pubescens*.

Remarks

Three Recent species from the New Zealand region are referable to *Thracia* (s. lat.): *Lyonsia vitrea* Hutton, 1873, here resurrected from synonymy and referred to subgenus *Odoncineta* O. G. Costa, 1829; *Thracia meridionalis* E. A. Smith, 1885, a new record for the region, here referred to *Crassithracia* Soot-Ryen, 1941; and *Thracia* (s. lat.) *vegrandis* P. Marshall & R. Murdoch, 1919 (not discussed herein: see Powell 1974: 200, 1979: 433).

Thracia reinga Crozier, 1966 from off the Three Kings Islands, northern New Zealand, is closely similar to *Tellimya ferruginosa* (Montagu, 1808), type species of *Tellimya* Brown, 1827 in gross shell morphology, although larger, and evidently belongs in Montacutidae. *Thracia reinga* is here referred to *Tellimya* together with the similar New Zealand species *Scintillona benthicola* Dell, 1956. Although strongly developed, the ligaments in *Montacuta substriata* (Montagu, 1808) and *M. tenella* (Lovén, 1846) (type species of *Montacuta* Turton, 1822 and *Decipula Friele*, 1875 respectively) are weaker than in *T. ferruginosa*, with resilifers less sunken and less oblique (Ockelmann 1965). *Tellimya ferruginosa* has a strongly developed, somewhat butterfly shaped, brown (non-calcified) ligament set on rather strongly oblique sunken resilifers (Fig. 1L). *Tellimya reinga* and *T. benthicola* both have large, strongly oblique, sunken resilifers, as does the similar North American species *Montacuta floridana* Dall, 1899 (type species of *Oorbitella* Dall, 1900) and they must have substantial ligaments too. The enlarged ligament in the montacutid genus *Montacutona* Yamamoto & Habe, 1959 is partly calcified (i.e. a lithodesma; Morton 1980).

Subgenus *Odoncineta* O. G. Costa, 1829

Odoncineta Costa, 1829: 14. Type species (by monotypy): *Tellina papyracea* Poli, 1791 (not Gmelin, 1791) = *Amphidesma phaseolina* Lamarck, 1818; Recent, Europe.

Thracia (*Odoncineta*) *vitrea* (Hutton, 1873) n. comb.

Figs 1A,D,H,K, 3A, 5A, 21A

Lyonsia vitrea Hutton, 1873a: 61; Hutton, 1878: 44; Hutton, 1880: 136.

Thracia vitrea. – Hutton, 1884: 514 (in part = '*Parilimya*' *neozelanica* (Suter, 1914)); Hutton, 1893: 75 (in part = *Asthenothaerus maxwelli* n. sp. (pl. 9, fig. 80) + '*P.*' *neozelanica*); Suter, 1913: 1024 (in part: pl. 62, fig. 15 = *A. maxwelli*); Dell, 1956: 41; Powell, 1957: 84 (in part: pl. 11, fig. 24 = *A. maxwelli*); Powell, 1962: 125 (in part: pl. 11, fig. 24 = *A. maxwelli*); Marshall, 1998: 145.

Eximiothracia vitrea. – Powell, 1937b: 61 (in part: pl. 11, fig. 24 = *A. maxwelli*); Powell, 1946: 63 (in part: pl. 11, fig. 24 = *A. maxwelli*).

Thracia (*Hunkydora*) *australica novozelandica*. – Powell, 1976: 131 (in part not Reeve, 1859: pl. 18, fig. 24 = *A. maxwelli*); Powell, 1979: 433 (in part not Reeve: pl. 79, figs 6, 7 = *A. maxwelli*).

NOT *Thracia vitrea*. – Odhner, 1924: 84 (= *A. maxwelli*).

Material examined

Syntypes. No locality data; type locality here selected as Wellington Harbour, New Zealand (4 fragmentary v, M.281).

Other material examined. SW of Cape Maria van Diemen, 34°41.9'S, 172°33.5'E, alive, 103 m (1pr, M.76043). Bay of Islands: 35°11.5'S, 174°15.5'E, 54–58 m (1v, M.95832); off Onewhero Bay, 35°14'S, 174°06'E, 18 m (1v, M.35568); off Onewhero Bay, 35°14'S, 174°05.5'E, 15 m (1v, M.44218); off Onewhero Bay, 35°14'S, 174°06'E, alive, 18 m (1pr, 1v, M.49478). Off Hen Island, 36°00.5'S, 174°43'E, alive, 59 m (1pr, M.43819). W of Plate Island, 37°39.1'S, 176°31.5'E, 64–59 m (1pr, 1v, M.67588). Off Motiti Island, alive, 46 m (7pr, M.39370). SE of Plate Island, 37°43.4'S, 176°38.5'E, alive, 59 m (3pr, M.65313). Off Motuhora Island, 25 m (2pr, 3v, M.39929). ENE of Tolaga Bay, 38°15.2'S, 178°38.6'E, 139 m (1v,

M.59820). Wellington Harbour, various stations (8pr, M.8000; 1pr, M.15940; 6v, M.15939; 8v, M.15941; 3pr, M.62798; 17pr, M.144103; 8pr, M.144123; 25pr, M.144136; 3pr, M.144160; 1v, M.14401). NE of Stephens Island, 40°31'S, 174°15'E, alive, 117–119 m (1pr, M.53756); 40°33'S, 174°07'E, alive, 132 m (1pr, M.53033). W of Kapiti Island, 40°44'S, 174°34'E, 146 m (1v, M.11306). Marlborough Sounds: Catherine Cove, Admiralty Bay, 40°53'S, 173°54'E, 40–44 m (2pr, M.55110); Admiralty Bay, 40°54'S, 173°56'E, alive, 44 m (2pr, 1v, M.55049); between West Entry Point and Duffers Reef, Pelorus Sound mouth, 40°57.5'S, 174°01.5'E, alive, 29 m (8pr, M.51506); Orchard Bay, Pelorus Sound mouth, 40°57.5'S, 174°03.5'E, alive, 26–29 m (3pr, 1v, M.54699); Orchard Bay, 40°58'S, 174°04'E, alive, 29 m (2pr, 1v, M.45133); Waitui Bay, 41°00.5'S, 174°11.0'E, alive, 15 m (2pr, 1v, M.51549); Port Gore entrance, 41°00.5'S, 174°15.0'E, alive, 15 m (7pr, M.51630); between Motuara Island and White Rocks, Queen Charlotte Sound, 41°05.5'S, 174°19.0'E, 15 m (8pr, 1v, M.54326); Titirangi Bay, Guards Bay, 41°01'S, 174°08'E, 4–9 m (1pr, M.149603); head of Anakoha Bay, Guards Bay, 41°02'S, 174°06'E, alive, 15–18 m (2pr, M.52177); Manaroa Bay, Pelorus Sound, alive, 5–18 m (10pr, M.144402); Otanerau Bay in East Bay, Arapawa Island, 41°11'S, 174°20'E, alive, 20–29 m (18pr, M.50830); Otanerau Bay in East Bay, 41°11'S, 174°20'E, 22–37 m (1v, M.54383); Double Bay, Kenepuru Sound (3v, M.18069). Akaroa Harbour entrance, 43°54'S, 172°57'E, alive, 13–15 m (1pr, M.108881). Stewart Island: Maori Beach (1v, M.3460); off Vaila Voe (2v, M.19293); Glory Inlet, 18–36 m (3v, M.19295).

Description

Shell up to 30 mm long, thin and brittle, whitish; left valve almost as inflated as the right, dorsoventrally shorter, and seated largely within its perimeter; umbones low, rounded, at approximately posterior one-third; periostracum very thin, translucent pale buff. Prodissoconch approximately 200 µm wide, strongly inflated (surface eroded). Dissoconch margins smoothly merging; anterior margin well rounded, posterior margin subtruncate, other margins broadly rounded; exterior posterior area distinctly flattened, elsewhere rather evenly rounded. Hinge line interrupted by narrow U-shaped space occupied by small lithodesma. Ligament strong, projecting externally, seated on large, prominent, rounded, similar chondrophores that descend from hinge line. Lithodesma butterfly shaped, small (width 0.8 mm in shell 13.7 mm long; 0.9 mm in shell 21.5 mm long), development slowing as shell enlarges, its resilifers elevated, oblique, steadily enlarging together with chondrophores as part of their supporting buttresses. Pallial sinus U-shaped, deep, depth 48%–51% of shell length. Anterior adductor scar considerably larger than posterior. Interior traversed by weak radial lines. Interior iridescent due to thin layer of nacre prisms. Exterior with low, irregular commarginal growth lines and wrinkles; flattened posterior area covered with minute, crowded granules, elsewhere a dulling microsculpture resembling irregular paving stones.

Distribution

North, South and Stewart islands, 0–146 m; taken alive at 15–132 m from mud (locally common; Fig. 5A).

Remarks

Practically since its introduction, the New Zealand species *Lyonsia vitrea* Hutton, 1873, has been variously confused with the parilimyid '*Parilimya*' *neozelanica* (Suter, 1914) and the superficially similar species *Asthenothaerus maxwelli* n. sp. (Thraciidae) and *Hunkydora novozelandica* (Reeve, 1859) (Myochamidae). The type material of *Lyonsia vitrea* (NMNZ) originally comprised four valves gummed to a glass plate. These valves are now fragmented, but the species involved is clearly indicated by valve outline in the gum on the plate, shell thinness, iridescence and microsculpture and the characteristic chondrophores. *Lyonsia vitrea* is here tentatively referred to *Thracia*, subgenus *Odoncineta*, because of close similarity to the European type species, *T. (O.) phaseolina* (Lamarck, 1818) in gross



Fig. 1. Shells of *Thracia*, *Asthenothaerus* and *Hunkydora* species and details of hinge areas. *A,D,H,K*, *Thracia* (*Odoncineta*) *vitrea* (Hutton, 1873): *A,H*, right (*A* upper) and left valve, length 18 mm, off Kau Point, Wellington Harbour (M.62798); *D*, dorsal view of pair, length 20 mm, between Somes Island and Eastbourne, Wellington Harbour (M.144136); *K*, ventral view of hinge area, lithodesma arrowed. *B,G*, *Thracia* (*Crassithracia*) *meridionalis* E. A. Smith, 1885: right valve (*B* upper), length 22.0 mm, and left valve, length 26.0 mm, Papanui Canyon, off Otago Peninsula, New Zealand, 490–540 m (M.158244). *C,E,I,J*, *Asthenothaerus maxwelli* n. sp.: *C,I*, right (*C* upper) and left valve, length 30.5 mm, Horseshoe Bay, Stewart Island (holotype, M.152678); *J*, juvenile, length 2.50 mm, off Patea, 40 m (M.53531). *F*, *Hunkydora novozelandica* (Reeve, 1859): dorsal view of pair, length 15 mm, SE of Three Kings Islands, 121 m (M.150896). *L*, *Tellimya ferruginosa* (Montagu, 1808): ventral view of hinge area, showing large, non-calcified ligament (arrow), Eldfisk Oil Field, North Sea, 70 m (Swedish Museum of Natural History, Stockholm). *M*, *Pendaloma micans* (Hedley, 1901): ventral view of hinge area, lithodesma arrowed, Pegasus Canyon, NE of Banks Peninsula, 622 m (M.90220). Scale bars: *K,M*, 1 mm; *L*, 200 μ m.

shell morphology. However, the New Zealand species differs markedly in being thinner and in that the interior is slightly, but distinctly, iridescent due the presence of a thin nacreous layer (thickness approximately 30 μm ; Fig. 3A). Although nacre has not been recorded from Thraciidae hitherto (Keen 1969b: 850; Taylor *et al.* 1973: 282), interior iridescence (presumably due to nacre) has, nevertheless, been recorded in *T. (s. lat.) myopsis* Beck in Møller, 1842 (Greenland) (Soot-Ryen 1941), *T. (Odoncineta) roumei* Cosel, 1995 (West Africa) (confirmed as interior by R. von Cosel, personal communication), and *T. (Eximiothracia) speciosa* Angas, 1869 (Australia) (Coan 1990a). The latter species is type of *Eximiothracia* Iredale, 1924, which Coan (1990a) has suggested is possibly synonymous with *Odoncineta*, despite indication that *T. (O.) phaseolina* is not iridescent. Whether or not *T. (O.) phaseolina* and other thraciids that are non-iridescent actually lack a thin nacreous layer (perhaps sandwiched within the shell wall) remains to be established by examination of shell cross-sections. Uncertain of relationships in this group, I follow Coan (1990a) in treating *Odoncineta* as a subgenus of *Thracia*, at rank equal with *Ixartia* Leach, 1852, *Homoeodesma* P. Fischer, 1887, *Crassithracia* Soot-Ryen, 1941 and *Cetothrax* Iredale, 1949.

Thracia (Odoncineta) vitrea is illustrated here for the first time (Figs 1A,D,H,K, 3A, 21A); all previously published illustrations purporting to represent it are actually of *Asthenothaerus maxwelli* n. sp. *Thracia (O.) vitrea* is separable from the previously named species *Hunkydora novozelandica* by the thinner shell, more posterior umbones, more strongly convex left valve, much deeper pallial sinus, relatively smaller lithodesma, exterior microsculpture of microscopic granules rather than crisp, commarginally elongate prisms and in having prominent matching chondrophores hanging from the hinge line of both valves.

Subgenus *Crassithracia* Soot-Ryen, 1941

Crassithracia Soot-Ryen, 1941: 19. Type species (by original designation): *Thracia crassa* Becher, 1886 = *T. septentrionalis* Jeffreys, 1872 (following Coan *et al.* 2000); Recent, North Atlantic. Introduced as a subgenus of *Thracia* Blainville, 1824.

Thracia (Crassithracia) meridionalis E. A. Smith, 1885 n. comb.

Figs 1B,G, 5C

Thracia meridionalis Smith, 1885: 68, pl. 6, figs 4–4b; Dell, 1990: 63, figs 109–111 (early references); Hain, 1990: 101, pl. 15, figs 7a,b; Branch *et al.* 1991: 51; Linse, 1997: 61; Linse & Brandt, 1998: 884; Cattaneo-Vietti *et al.* 2000: 176; Troncoso *et al.* 2001: 112, fig. 42.

Mysella? truncata Thiele, 1912: 230, pl. 18, fig. 18.

Mysella? frigida Thiele, 1912: 230, pl. 18, fig. 19.

Material examined

Syntypes of Thracia meridionalis. Balfour Bay, Royal Sound, Kerguelen Is. (BMNH 1887.2.9.2473, 1887.2.9.2473a-b and 2474, 2475).

Holotype of Mysella truncata. Gauss Station, Davis Sea, Antarctica (1v, ZMB 63110).

Holotype of Mysella frigida. Gauss Station, Davis Sea, Antarctica (ZMB 63111).

Other material examined. **Antarctica:** several hundred specimens (34 lots NMNZ); **New Zealand:** Papanui Canyon, off Otago Peninsula, 45°50'S, 171°01'E, 490–540 m (5v, M.158244).

Distribution

Circum-Antarctic and off Otago Peninsula, New Zealand, 5–752 m; taken alive at 5–220 m (Fig. 5C).

Remarks

The Papanui Canyon valves fall within the range of variation of Antarctic specimens of this common, widely distributed species and represent both a new record for the New Zealand region and the northern-most record for the species. No other specimens have been recorded from scores of rich samples dredged from Papanui Canyon or other submarine canyons off Otago Peninsula, suggesting that the shells possibly date from a period when sea temperatures were lower. The sample containing them was extremely and unusually rich, both in number of species and individuals, although almost entirely empty shells, and seems likely to have accumulated over a long period of time, probably hundreds or even thousands of years (but certainly post-dating last glacial maximum).

Thracia meridionalis is here referred to subgenus *Crassithracia* because of its similarity to *T. septentrionalis* in shell morphology. It is even closer to the circum-Arctic species *T. devexa* G. O. Sars, 1878, which also seems likely to belong here. The ligament in *T. septentrionalis* and *T. devexa* is much stronger than in *T. vitrea*, with resilifer rims that are long and upturned rather than short and downturned, the ligament in *T. vitrea* projecting further ventrally.

Genus *Asthenothaerus* Carpenter, 1864

Asthenothaerus Carpenter, 1864: 311. Type species (by monotypy): *Asthenothaerus villosior* Carpenter, 1864; Recent, eastern Pacific.

Asthenothaerus maxwelli n. sp.

Figs 1C,E,I,J, 3B, 4A, 5B, 21B

Thracia vitrea. – Hutton, 1893: 75 (in part not Hutton, 1873 + '*Parilimya*' *neozelanica* (Suter, 1914)), pl. 9, fig. 80; Suter, 1913: 1024 (in part not Hutton), pl. 62, fig. 15; Odhner, 1924: 84 (not Hutton).

Eximiothracia vitrea. – Powell, 1937b: 61 (in part not Hutton), pl. 11, fig. 24; Powell, 1946: 63 (in part not Hutton), pl. 11, fig. 24

Thracia vitrea. – Dell, 1956: 41 (in part not Hutton); Powell, 1957: 84 (in part not Hutton), pl. 11, fig. 24; Powell, 1962: 125 (in part not Hutton), pl. 11, fig. 24.

Thracia (Hunkydora) australica novozelandica. – Powell, 1974: 200, figs 13, 14 (not Reeve, 1859); Powell, 1976: 131 (in part + *T. vitrea*), pl. 18, fig. 24; Powell, 1979: 433 (in part + *T. vitrea*), pl. 79 figs 6, 7 only.

Parvithracia cuneata. – Powell, 1979: 434 (Auckland Islands record).

Thraciidae sp. 1 Spencer *et al.* (in press).

Material examined

Holotype. Horseshoe Bay, Stewart Island, New Zealand, Apr. 1963, E. C. Smith (pr, M.152678).

Paratypes. New Zealand, Stewart Island, Horseshoe Bay, Apr. 1963, E. C. Smith (5pr, 5v, M.16872); Horseshoe Bay (3pr, M.15302; 2pr, 10v, M.30985; 12pr, M.132839).

Other material examined. *Fossil*: Landguard Bluff, Wanganui, Late Pleistocene (Castlecliffian) (1pr, 8v, M.13080). *Recent*: Off Rangaunu Bay, 34°49.6'S, 173°15.0'E, alive, 23 m (1pr, M.150895). Off Takau Bay, 35°10'S, 174°11'E, 80 m (2v, M.43695). Bay of Islands: off Twin Rocks, 35°10'S, 174°18'E, 46–73 m (1v, M.154732); off island at entrance to Deep Water Cove, 35°11.9'S, 174°17.1'E, 47–49 m (2v, M.152674); between Hope Passage and Deepwater Cove, 35°12'S, 174°18'E, 37–40 m (2v, M.41416); Bamboo Bay, Moturua Island, 35°13.9'S, 174°11.3'E, 4–6 m (1v, M.40840). Schooner Bay, Great Barrier Island, 15 m (1pr, M.155466); off Cuvier Island, 49–73 m (1v, M.3458). Off Rurima Rocks, 26 m (2, M.152676). Ranfurly Bank, East Cape, 37°32.8'S, 178°48.7'E, 94 m (1pr, M.60728); 37°33.1'S, 178°49.5'E, 94–89 m (3v, M.64820). N of Motuhora Island, 37°35.9'S, 176°59.5'E, 179–139 m (1v, M.60572). N of New Plymouth, 38°55.0'S, 174°09.3'E, 48 m (1pr, M.150894). S of Patea, alive, 39°56'S,

174°26'E, 40 m (11pr, M.53531). SW of Wanganui, 40°11'S, 174°49'E, 58–64 m (2pr, M.50776). Off D'Urville Island: off Puangiangi Island, 15–22 m (1pr, M.100530); Long Beach (3v, M.11936). Titirangi Bay, Guards Bay, 41°01'S, 174°08'E, 4–9 m (5v, M.54071). Head of Titirangi Bay, beach (18v, M.40656). Queen Charlotte Sound, 15 m (1pr, M.132954). Manaroa Bay, Pelorus Sound, 22 m (4pr, 5v, M.18354). Mernoo Bank, W Chatham Rise, 43°06.1'S, 175°20.5'E, 153 m (1v, M.65072); 42°51.9'S, 175°26.5'E, 183 m (1v, M.15437); 42°59.4'S, 175°30.5'E, 112 m (2v, M.15438). Chatham Islands: N of The Sisters, 43°32.5'S, 176°47.5'W, 60 m (1v, M.12410); E of Forty Fours, 44°04'S, 175°23.5'W, 238 m (1v, M.10872). Head of Waitaki Canyon, off Oamaru, 45°10'S, 171°30'E, 293–256 m (1v, M.51265). SW of Hare's Ears, Doubtful Sound, 45°17.2'S, 166°49.3'E, 146 m (4v, M.58743). Off Taiaroa Head: 45°44'S, 171°02'E, 137 m (2v, M.11083); Taiaroa Canyon, 45°45.4'S, 171°05'E, 549 m (2v, M.152675); NE of Cape Saunders, 45°50'S, 170°56'E, 105 m (3v, M.45373); Papanui Canyon, 45°51'S, 171°00'E, 348–220 m (1v, M.74868); 45°51'S, 170°59'E, 220 m (1v, M.131304). Off NW end of Cooper Island, Dusky Sound, 45°44.0'S, 166°47.5'E, 12 m (1v, M.135529). Opposite Sandy Point, Long Sound, 46°02.16'S, 166°45.88'E, alive, 20 m (1pr M.141156). Off Taieri, 46°07.0'S, 170°39.0'E, 87 m (8v, M.58904). Stewart Island: Easy Harbour, 47°09'S, 167°34'E, 7–20 m (1v, M.26561); North Arm, Port Pegasus, 47°11'S, 167°41'E, 37–44 m (2v, M.26725); North Arm, 47°11'S, 167°41'E, 40–46 m (1v, M.42401); S of Port Pegasus, 47°18.5'S, 167°42.5'E, 119 m (1v, M.26514); Mason Bay (1pr, M.19297); Halfmoon Bay (5v, M.19296); off Vaila Voe (3pr, M.155168); Maori Beach (2v, M.3457); Golden Bay (1pr, M.19294). Off Bounty Islands, 49°40.19'S, 178°44.30'E, alive, 113 m (1pr, 8v, M.150075). Off Antipodes Islands, 49°40'S, 178°52'E, 86–95 m (3v, M.39558); 49°40'S, 178°53'E, 103 m (5v, M.39558). N of Auckland Islands, 174 m (2v, AIM 131367). Between Dees Head and Tucker Point, Auckland Islands, 26–27 m (4v, M.16744).

Description

Shell up to 46 mm long, longer than high, thin, white, hinge edentulous, no external ligament, lithodesma well developed; periostracum very thin, olive green. Prodissoconch 200 µm wide, PI globular, 150–170 µm wide. Right valve approximately 1% larger than left, approximately 8% thicker, left valve sitting within its perimeter; beaks at approximately posterior one-third, opisthogyrous. Posterodorsal margin straight, anterior margin rounded, anterodorsal and ventral margins more broadly rounded, margins smoothly merging; posterior margin obliquely truncate, separated by rounded angulations. Externally convex, right valve more inflated than left; posterior area defined by rounded angulation, weakly concave or flat; sculpture of weak, irregular, rounded commarginal ridges; microsculpture of minute, crisp, crowded granules resembling irregular paving stones (not separated by wavy radial striae), coarser on posterior area. Lithodesma very large relative to those in most other thraciids, strong, somewhat butterfly shaped; resilifers oblique, narrowly subtriangular, posterior margin straight or broadly concave; anterior margin broadly convex, elevated, rim undercut. Anterior adductor scar curved, narrowly elliptical; posterior scar subcircular; pallial sinus depth 44%–48% of adult shell length, anterior margin rounded.

Distribution

Late Pleistocene (Castlecliffian) – Recent. North, South, Stewart, Auckland, Antipodes, Bounty and Chatham Islands and Chatham Rise, 0–293 m; taken alive (juveniles) at 20–40 m from sand and sandy mud (Fig. 5B).

Remarks

Asthenothaerus maxwelli closely resembles the type species of *Asthenothaerus* (Coan 1990a: 39, figs 32, 33) in gross facies, including the characteristic lack of an external ligament. However, the New Zealand species differs markedly in attaining more than three times the size. Specimens from off the Auckland and Antipodes Islands (length up to 46 mm) attain larger size than specimens from elsewhere in the New Zealand region, but

are otherwise indistinguishable. As indicated by the synonymy, *A. maxwelli* has been confused with both *Thracia vitrea* and *Hunkydora novozelandica*, the three species being sympatric, but apparently asyntopic. Although quite similar to *T. vitrea* in shell shape, *A. maxwelli* differs markedly in that the ligament is fully internal, in lacking chondrophores and in that the lithodesma is very much larger and fully functional at all stages of growth (development retarded from an early stage of growth in *T. vitrea*). *Asthenothaerus maxwelli* differs further in attaining a larger size (length up to 46 mm as against 30 mm) and in that the shell is thicker and considerably stronger. *Asthenothaerus maxwelli* differs principally from *H. novozelandica* in having a more strongly convex left valve with beaks further posterior, in lacking a posterodorsal groove on the right valve for seating the corresponding margin of the left valve and in that the external microscopic granules are thinner, mostly longer and separated by wavy radial striae.

Hutton (1893) treated *Thracia granulosa* Hutton, 1873 (1873b) as a synonym of *T. vitrea* and illustrated a specimen of what is clearly *A. maxwelli*, which is not uncommon at Landguard Bluff, Wanganui. When providing the substitute name *T. neozelanica* for *T. granulosa* Hutton, 1873 (not A. Adams & Reeve, 1850), Suter (1914) correctly indicated that *T. neozelanica* is an entirely different species, as indeed is clear from Hutton's original description. *Thracia neozelanica*, which also occurs Recent (16 lots NMNZ), belongs in the Parilimyidae and is currently grouped in *Parilimya* Melvill & Standen, 1899 for want of a more appropriate location (Beu and Maxwell 1990).

Asthenothaerus maxwelli is similar to the eastern Australian myochamid *Hunkydora australica* (Reeve, 1859) in shape (two syntypes BMNH 1962695, Moreton Bay, Queensland; the larger figured by Fleming 1951, figs 1, 2), but the latter is immediately separable by the characteristic microsculpture (external shell layer) of fine commarginal striae and wavy radial striae.

Etymology

After Philip Maxwell of Waimate (formerly NZGS), in appreciation of his friendship and outstanding contributions to molluscan systematics and palaeontology.

Genus *Barythaerus* n. gen.

Type species: *Myadora biconvexa* Powell, 1927; Recent, southern New Zealand.

Diagnosis

Shell small (maximum lengths 5.10 and 5.50 mm), stout, beaks at posterior one-third to one-quarter, no external ligament, resilifers sunken, lithodesma ovate, prominent tooth in front of beak on right valve only, no corresponding socket in left valve. Interior not nacreous, pallial sinus depth 33%–41% of shell length. Externally with irregular, paving stone-like microsculpture.

Remarks

The two *Barythaerus* species resemble *Parvithracia* species in having a prominent anterior tooth on the right valve, but differ in being stouter and more oblique and in having an irregular paving stone-like exterior dissoconch microsculpture and markedly opisthogyrous beaks. *Barythaerus* and *Parvithracia* species differ further in the shape of the lithodesma,

which is more or less ovate in *Barythaerus*, rather than butterfly shaped as in *Parvithracia*. *Asthenothaerus* species are similar in shape but lack the prominent tooth in front of the beak on the right valve. *Parvithracia* Finlay, 1926 and *Lampeia* MacGinitie, 1959 are less stout, have considerably shorter anterior ends and a butterfly-shaped lithodesma. The resilifers are simple and not buttressed as in *Lampeia* (Kamanev and Nadtochy 1998). A few valves from off the Chatham Islands and East Otago (Thraciidae sp. 4 of Spencer *et al.* in press; e.g. M.10860, M.48859) represent an additional species. See additional remarks under *Grippina* (below).

Etymology

From the Greek *barys* (heavy) and *thaeros* (hinge); gender masculine.

Barythaerus biconvexus (Powell, 1927)

Figs 2A,C, 3C, 4B, 5D, 21C

Myadora biconvexa Powell, 1927: 123, pl. 23, fig. 9; Powell, 1979: 432.

Material examined

Syntypes. Off Puysegur Point, New Zealand, 46°11'S, 166°30'E, 183 m, Dec. 1908, SS *Rakiura* (12v, CM M.861, M.862)

Other material examined. Off Taieri, 46°07.0'S, 170°39.0'E, 87 m (1v, M.66069); 46°15.0'S, 170°29.0'E, 91 m (3v, M.66168). Off Puysegur Point, 46°11'S, 166°30'E, alive, 183 m (and 311 m – Powell 1927) (1pr, many v, M.7407). SE of Nugget Point, 46°40'S, 170°00'E, 140 m (2v, M.65941). Stewart Island: off Tehatatahi Island, 46–64 m (1v, M.19877); off Halfmoon Bay, 27–55 m (2v, M.19873); Halfmoon Bay, 27 m (1v, M.19874); off Garden Point, 22 m (2v, M.19875); off Poutama Island, 47°16'S, 167°23'E, alive, 55 m (1pr, 15v, M.19878); off Big Island, South Cape, 73–82 m (2v, M.19876).

Description

Shell up to 5.10 mm long, strongly inaequilateral, oblique, umbones at approximately posterior one-sixth, weakly to very strongly thickened, moderately inflated, 1.48–1.57× longer than high, translucent white. Prodissoconch approximately 230 µm wide, smooth; PI approximately 170 µm wide, globular. Dissoconch with shallow but distinct lunule, anterodorsal margin more or less flat or very weakly convex, posterodorsal margin broadly concave, anterior and posterior margins well rounded, ventral margin very broadly rounded or more or less flat; exterior broadly convex. Right valve with strong anterior hinge tooth, strongly shelved anteriorly and posteriorly to seat elevated antero- and posterodorsal margins of left valve; hinge area of both valves divided by broad triangular space. Lithodesma stout, short, thick; supporting plates simple, oblique, elliptical. Interior glossy, with weak radial lines; pallial sinus and pallial line well defined, sinus depth 33%–34% of shell length. Adductor and anterior pedal retractor muscle scars sharply defined. Exterior with low, rounded, anterodorsal angulations that bound concave lunule; tightly rounded to concave escutcheon; microsculpture resembling irregular paving stones, imparting a dull sheen.

Distribution

Southern South Island and Stewart Island, 27–311 m; taken alive at 55–183 m from bryozoan/shell substrata (Fig. 5D).

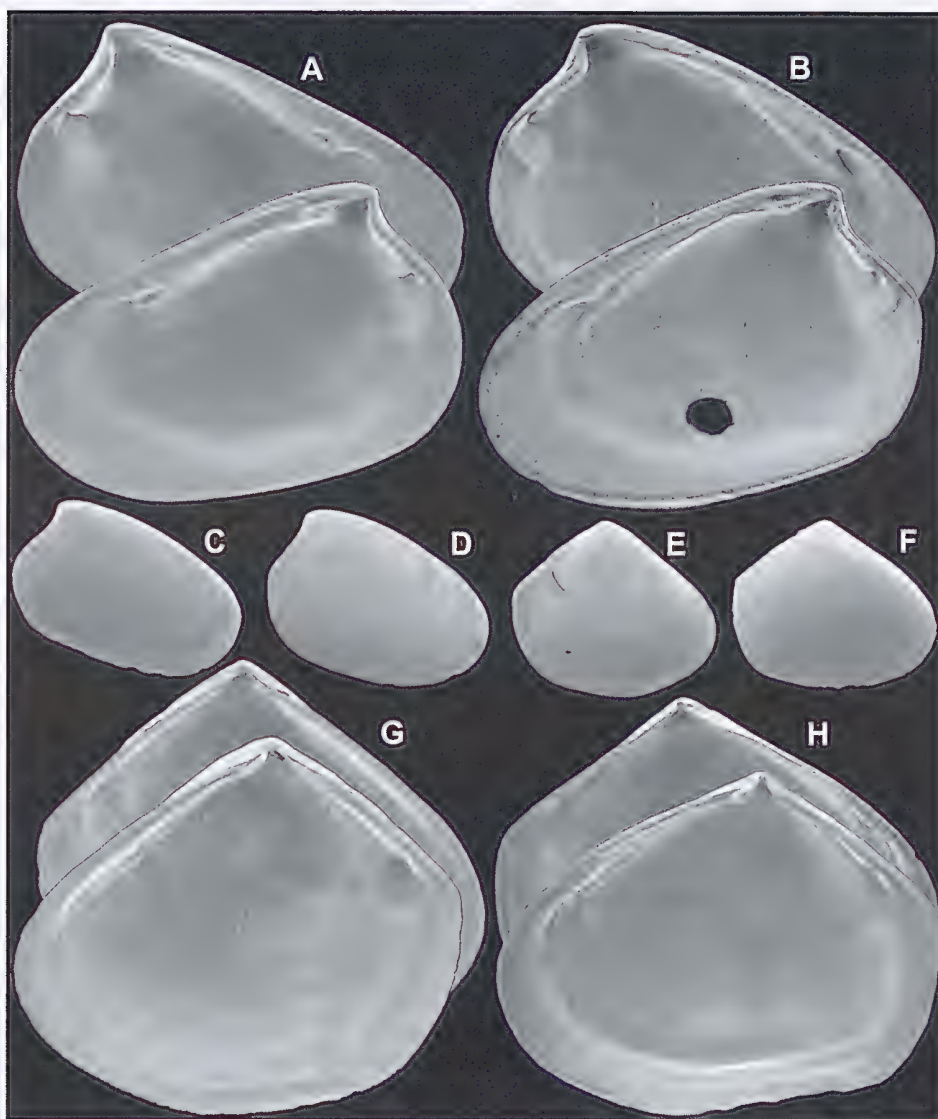


Fig. 2. Shells of *Barythaerus* and *Parvithracia* species. *A,C*, *Barythaerus biconvexus* (Powell, 1927): left (*A* upper) and right valve, off Poutama Island, Big South Cape Island, Stewart Island, 55 m (M.19878). *B,D*, *Barythaerus cuneatus* (Powell, 1937): left valve (*B* upper), length 5.30 mm, and two right valves, lengths 4.60 mm (*B* lower) and 5.00 mm (*D*), 22 km ENE of Great Island, Three Kings Islands, 200 m (M.144363). *E,G*, *Parvithracia* (*s. str.*) *suteri* (Finlay, 1927): left (*G* upper) and right valves, length 3.25 mm, North Arm, Port Pegasus, Stewart Island, 37–44 m (M.44790). *F,H*, *Parvithracia* (*s. str.*) *ampla* n. sp.: holotype, left (*H* upper) and right valve, length 6.60 mm, Saunders Canyon, off Otago Peninsula, 457 m (M.9125).

Remarks

Barythaerus biconvexus is redescribed here to facilitate direct comparison with *B. cuneatus*. *Barythaerus biconvexus* attains more than twice the size of its type specimens (length up to 5.1 mm).

Barythaerus cuneatus (Powell, 1937)

Figs 2B,D, 3D, 4C, 5E, 21D

Parvithracia cuneata Powell, 1937a: 174, pl. 46, fig. 9; Powell, 1979: 434, fig. 117/4 (in part: Auckland Islands record = *Asthenothaerus maxwelli*).

Material examined

Holotype. Off Three Kings Islands, New Zealand, 34°11.6'S, 172°10.9'E, 92 m, 17 Aug. 1932, *RRS Discovery II* (1v, BMNH 1962949).

Other material examined. Off Three Kings Islands: King Bank, 33°57.0'S, 172°19.0'E, 128 m (8v, M.149501); King Bank, 33°57.4'S, 172°19.4'E, alive, 128–123 m (1pr, 34v, M.149568); 37 km NE of Great Island, 33°58.0'S, 172°30.6'E, 550 m (1v, M.149505); 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (2v, M.59551); Three Kings Trough, 34°00'S, 171°55'E, 805 m (6v, M.17519); 34°01'S, 172°07'E, 622 m (2v, M.35000); 13 km N of Great Island, 34°01.8'S, 172°12.0'E, 508 m (36v, M.59548); Middlesex Bank, 34°02.0'S, 171°44.0'E, 246–291 m (3v, M.149566); Middlesex Bank, 34°02.1'S, 171°45.8'E, 221–206 m (3v, M.149503); 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (3v, M.144363); off North-east Island, 34°08.5'S, 172°11'E, 102 m (3v, M.34549); 34°11'S, 172°10'E, 91 m (1v, M.144364). NW of Cape Reinga, 34°14.2'S, 172°32.4'E, 100 m (6v, M.59552). Off Spirits Bay, 34°18.36'S, 172°49.39'E, alive, 68 m (1pr, many v, M.149504). N of Cape Reinga, 34°21'S, 172°37'E, 88 m (1v, M.36011). Off Spirits Bay, 34°21.60'S, 172°43.19'E, 48 m (2v, M.153096). NW of Cape Reinga, 34°22.8'S, 172°24.6'E, 121 m (1v, M.149567).

Description

Shell up to 5.5 mm long, strongly inequilateral, oblique, umbones at approximately posterior one-fifth, modestly thickened, moderately inflated, 1.41–1.50× longer than high, translucent white. Prodissoconch approximately 250 µm wide, smooth; PI approximately 170 µm wide, globular. Dissoconch with shallow but distinct lunule, anterodorsal margin very broadly convex, posterodorsal margin shallowly concave, anterior margin well rounded, posterior and ventral margins broadly rounded, exterior broadly convex. Right valve with strong anterior hinge tooth, shelved anteriorly and posteriorly to seat elevated antero- and posterodorsal margins of left valve; hinge area of both valves divided by broad triangular space. Lithodesma stout, broad; supporting plates simple, oblique, elliptical. Interior glossy, with weak radial lines; pallial sinus and pallial line well defined, sinus depth 38%–41% of shell length. Adductor and anterior pedal retractor muscle scars sharply defined. Exterior with low, rounded, anterodorsal angulations that bound concave lunule; tightly rounded to concave escutcheon; microsculpture resembling irregular paving stones, imparting a dull sheen.

Distribution

Off Three Kings Islands and off Spirits Bay, 68–805 m; taken alive at 68–128 m from comminuted bryozoan and shell substrata (Fig. 5E).

Remarks

Barythaerus cuneatus is extremely similar to *B. biconvexus* in gross facies, differing principally in having a lighter hinge area, a deeper pallial sinus and in the shape of the lithodesma; the great majority of specimens differ further in that the hinge tooth on the right valve is shorter, yet projects further ventrally, the shell is higher relative to the length and the shell wall is thinner. The two species are allopatric.

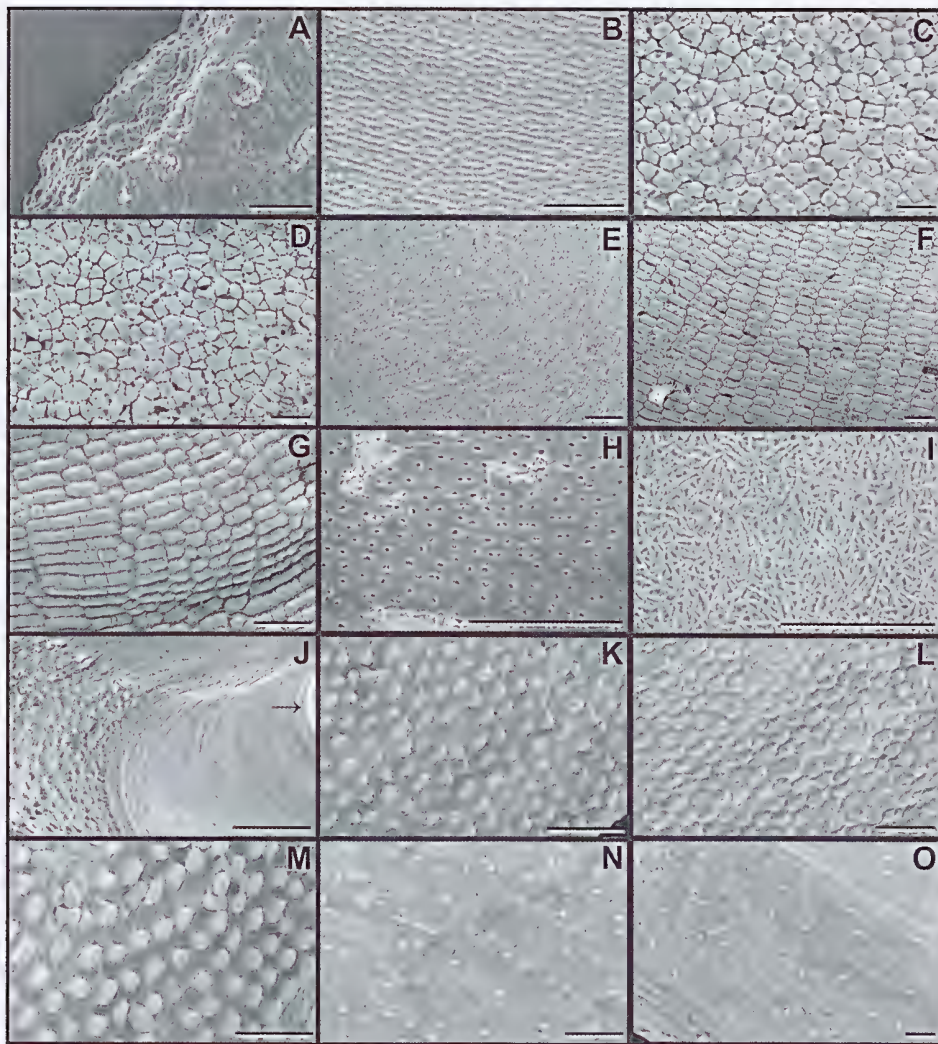


Fig. 3. Dissoconch shell structure and microsculpture of Thraciidae, Myochamidae and Cuspidariidae (exterior, right valve and adult unless indicated). *A*, *Thracia* (*Odoncineta*) *vitrea* (Hutton, 1873), inner surface of central dissoconch, obliquely fractured to show nacre prisms; Guards Bay, Marlborough, 15–18 m (M.52177). *B*, *Asthenothaerus maxwelli* n. sp., juvenile, off Patea, 40 m (M.53531). *C*, *Barythaerus biconvexus* (Powell, 1927), off Poutama Island, Big South Cape Island, Stewart Island, 55 m (M.19878). *D*, *Barythaerus cuneatus* (Powell, 1937) (M.144363). *E*, *Trigonthracia mimica* n. sp., holotype, Doubtful Sound entrance, 117–128 m (M.155019). *F*, *Myadoropsis wairua* n. sp., holotype, N of Three Kings Islands, 622 m (M.152686). *G*, *Myochama tasmanica* (Tenison Woods, 1877), left valve, costate area of pre-cementation stage, Arch Pinnacle, Prince's Islands, Three Kings Islands, 40 m (M.117130). *H,I*, *Pseudogrippina wanganella* n. sp., holotype (*I* = interior), Wanganella Bank summit, Norfolk Ridge, 113 m (M.152681). *J,K*, *Plectodon lepidus* n. sp., edge of prodissoconch (arrow) and early dissoconch (*J*) and adult (*K*), off E side of Mayor Island, 59–74 m (M.152682). *L*, *Plectodon pruinosus* n. sp., holotype, Middlesex Bank, NW of Three Kings Islands, 98–103 m (M.152683). *M*, *Plectodon regalis* n. sp., holotype, off Three Kings Islands, 91 m (M.152684). *N*, *Rhinoclama* (*Austroneaera*) *brevirostris* (Powell, 1937), SE of Great Island, 173–178 m (M.144426). *O*, *Rhinoclama* (*Austroneaera*) *raoulensis* (Powell, 1958), off Meyer Island, Raoul Island, Kermadec Islands, 27–22 m (M.225814). Scale bar: *A*, 20 μ m; others, 50 μ m.

Genus *Parvithracia* Finlay, 1926

Parvithracia Finlay, 1926: 461. Type species (by original designation): *Montacuta triquetra* Suter, 1913, not Verrill & Bush, 1898 (preoccupied) = *Parvithracia suteri* Finlay, 1927; Recent, New Zealand.

Remarks

Kamanev (2002) has recently introduced *Pseudoasthenothaerus* as a new subgenus of *Parvithracia* for species with a lunule that lacks an internal groove beside the posterodorsal margin and that have resilifers supported by columnar buttresses. Whereas *P. ampla* n. sp. has characteristics of *Parvithracia* (s. str.), *P. melchior* n. sp. and *P. fragilissima* n. sp. resemble *Pseudoasthenothaerus* species in lacking an internal groove beside the posterodorsal margin, but the resilifer plate is not supported by pillars and there is no lunule.

Parvithracia (s. str.) *suteri* Finlay, 1927

Figs 2E, G, 4E, 7A, 21E

Montacuta triquetra Suter, 1913: 915, pl. 53, fig. 7a (not Verrill & Bush, 1898 (preoccupied)).

Parvithracia triquetra. – Finlay, 1926: 461.

Parvithracia suteri Finlay, 1927: 529 (replacement name for *Montacuta triquetra* Suter, 1913); Dell, 1956: 167 (in part = *P. ampla* n. sp.); Powell, 1979: 434, fig. 117/3.

Parvithracia (*Parvithracia*) *suteri*. – Kamanev, 2002: 109, figs 2–10.

Material examined

Lectotype (Borcham 1959: 21). Port Pegasus, Stewart Island, New Zealand, 33 m (NZGS TM 399).

Other material examined. SE of Great Island, Three Kings Islands, 34°14.8'S, 172°13.6'E, 173–178 m (8v, M.149537). N of North Cape: 34°18'S, 173°02'E, 137 m (1v, M.3060); SE of Three Kings Islands, 34°20.2'S, 172°21.8'E, 121 m (7v, M.149532); 34°20.0'S, 173°06.6'E, 163–168 m (1v, M.149545). N of Kerr Point, Tom Bowling Bay, 34°22.01'S, 173°00.20'E, 89 m (1v, M.155120). NW of Cape Reinga, 34°22.8'S, 172°24.6'E, 121 m (4v, M.149542). E of North Cape, 34°23.0'S, 173°12.6'E, 447–357 m (1v, M.149538). E of North Cape, 34°25.0'S, 173°13.1'E, 327–257 m (30v, M.149536). Great Exhibition Bay: 34°33.4'S, 173°04.8'E, 63 m (2v, M.113191); 34°33.6'S, 173°04.9'E, 66 m (1v, M.149540). SW of Cape Maria van Diemen, 34°41.9'S, 172°33.5'E, 103 m (1v, M.149541). Off Rangaunu Bay, 34°42.8'S, 173°14.5'E, 63 m (10v, M.155117). Off Whangaroa Bay, 34°54.0'S, 173°42.6'E, alive, 83 m (2pr, 30v, M.155118). Off Cape Brett, 35°08'S, 174°12.5'E, alive, 80 m (2pr, 30v, M.35716). Off Twin Rocks, 35°10'S, 174°18'E, 46–73 m (21v, M.42182). Off Takau Bay, 35°10'S, 174°11'E, 80 m (13v, M.43650). Off Ahipara, 35°10.4'S, 172°35.4'E, 233 m (2v, M.149546). Bay of Islands: 35°11.2'S, 174°16.7'E, alive, 58–64 m (15pr, 6v, M.96116); 35°11.5'S, 174°15.5'E, 54–58 m (1v, M.131108); 35°11.6'S, 174°16.5'E, 54 m (2v, M.95923); Deepwater Cove entrance, 35°12'S, 174°18'E, 46 m (3v, M.41697). Off Poor Knights Islands: 35°22'S, 174°43'E, 146 m (30v, M.35141); 35°28'S, 175°03'E, 282 m (1v, M.36066); 35°29'S, 174°43.5'E, 110 m (4v, M.74370); 35°32'S, 174°41'E, 121–113 m (18v, M.35829). Off Hen Island: 35°58.5'S, 174°44'E, 62 m (3pr, 7v, M.43937); 36°00.5'S, 174°43'E, 59 m (5pr, 8v, M.43821). Off Aldermen Islands: 37°00.8'S, 176°12.3'E, alive, 178–248 m (10pr, 15v, M.66634); 165 m (1v, M.44387). Off Mayor Island: 37°11.5'S, 176°10.0'E, alive, 198–273 m (2pr, M.66600); 37°16.7'S, 176°17.5'E, 104–109 m (1pr, 2v, M.67389); 37°18.9'S, 176°16.2'E, 59–74 m (1v, M.65729). Rungapapa Knoll, 37°33.8'S, 176°59.0'E, W of White Island, 188–228 m (1v, M.113535). Off Plate Island, 37°39.4'S, 176°34.4'E, 82 m (1v, M.67744). Ranfurly Bank, East Cape: 37°32.8'S, 178°48.7'E, 94 m (many v, M.60799); 37°33.1'S, 178°49.5'E, alive, 94–89 m (2pr, 30v, M.71422); 37°33.4'S, 178°48.3'E, alive, 106–103 m (1pr, 40v, M.71654); 37°36.7'S, 178°51.6'E, 56–63 m (2v, M.149539); 37°37.8'S, 178°52.4'E, 50–72 m (1v, M.96195); 37°38.5'S, 178°56.4'E, 153–143 m (21v, M.149534). Off Raglan Harbour: 37°48.0'S, 174°14.7'E, 103 m (1v, M.149535); 37°48.0'S, 174°14.0'E, 103 m (3v, M.149533). N of New Plymouth, 38°40.2'S, 174°03.9'E, alive, 88 m (4pr, 3v, M.149544). Off Cape Kidnappers, 39°52.8'S, 177°36.5'E, alive, 785–882 m (3pr, 2v, M.155115). S of Waverley, 40°10'S, 174°40'E, 77–82 m (4v, M.50645). W of Rangitikei R. mouth, 40°16'S, 174°58.5'E, alive, 75 m (4pr, 1v, M.53286). NE of Stephens Island, 40°33'S, 174°07'E, 132 m (1pr, M.53071). N of Kapiti Island, 40°38'S, 174°54.5'E, alive, 91 m (2v,

2pr, M.52902). E of Stephens Island, 40°42'S, 174°10.6'E, 106 m (2pr, M.7771). Off Palliser Bay, 41°35'S, 175°04'E, 128–146 m (1pr, 2v, M.44307); SE of Cape Campbell, 42°00.8'S, 174°41.0'E, alive, 939–1019 m (3pr, M.60459). Pegasus Canyon, 43°31.0'S, 173°30.5'E, alive, 256–293 m (1pr, M.94783). Milford Sound: 44°36.0'S, 167°49.0'E, 123 m (6v, M.10359); entrance sill, 44°36.42'S, 167°50.47'E, 117 m (6v, M.11423). Head of Waitaki Canyon, off Oamaru, 45°10'S, 171°30'E, 293–256 m (2v, M.51322). Thompson Basin floor, Thompson Sound, 45°14.38'S, 166°58.87'E, 340–362 m (3, M.150518). Doubtful Sound entrance, 45°16', 166°48', alive, 117–128 m (13pr, M.58625). Bradshaw Basin floor, Bradshaw Sound, 45°17.3'S, 167°02.6'E, 415 m (1pr, 4v, M.138387). Doubtful Sound: Utah Basin floor, 45°17.9'S, 166°55.5'E, 400 m (2v, M.138681); Seymour Basin, Malaspina Reach, 45°18.15'S, 167°00.64'E, 107 m (2pr, M.147072); Seymour Basin, 45°18.90'S, 167°00.64'E, 94 m (1v, M.147099); Seymour Basin, 45°18.21'S, 167°00.50'E, 64 m (1v, M.147128); Seymour Basin, 45°18.21'S, 167°00.87'E, alive, 94 m (6pr, 5v, M.147169); Seymour Basin, 45°18.27'S, 167°00.69'E, 115 m (4v, M.147231). Off Chatham Point, upper Breaksea Sound, 45°33'S, 166°53'E, 42 m (1v, M.139727). Off Taiaroa Head: Karitane Canyon, 45°37.5'S, 171°03'E, 420 m (2v, M.45618); head of Karitane Canyon, 45°38.5'S, 171°05.0'E, alive, 585–530 m (4pr, 4v, M.51091). Cook Channel, Dusky Sound, 45°46.0'S, 166°43.0'E, 44 m (1v, M.135465). North Arm, Port Pegasus, Stewart Island, 47°11'S, 167°41'E, alive, 37–44 m (many pr, M.44790).

Distribution

Three Kings, North, South, Stewart and Chatham Islands, 33–1019 m; taken alive at 37–549 m from mud (Fig. 7A).

Remarks

Parvithracia suteri is distinctive in its small size (length rarely greater than 4 mm), subtriangular outline, subcentral beaks, obliquely subtruncate posterior end and strong anterior hinge tooth on the right valve. The prodissococonch (Fig. 4E) is smooth, approximately 180 µm wide and the PI is approximately 170 µm wide and globular.

Parvithracia (s. str.) *ampla* n. sp.

Figs 2F,H, 4F, 7B, 21F

Parvithracia suteri. – Dell, 1956: 167 (in part).

Material examined

Holotype. Saunders Canyon, off Otago Peninsula, New Zealand, 45°55.2'S, 170°56.4'E, alive, 457 m, 16 Jan. 1954, MV *Alert* (pr, M.9125).

Paratypes. Off Gable End Foreland, 38°38.7'S, 178°41.1'E, alive, 755–725 m (1pr, M.155114). Off Cape Kidnappers, 39°52.8'S, 177°36.5'E, alive, 785–882 m (4pr, M.155115). SE of Cape Campbell, 42°00.8'S, 174°41.0'E, alive, 939–1019 m (3pr, M.60459). Wall of Pegasus Canyon, NE of Banks Peninsula, 43°14'S, 173°39'E, alive, 1006–512 m (2pr, 2v, M.52890). Chatham Rise: 43°32'S, 178°38'E, 549 m (1v, M.10866); 43°38'S, 177°19'E, 531 m (2v, M.10865); E of Forty Fours, 44°04'S, 175°23.5'E, alive, 238 m (1pr, M.42286). Head of Waitaki Canyon, off Oamaru, 45°10'S, 171°30'E, alive, 293–256 m (8v, M.155152). Off Taiaroa Head: Karitane Canyon, 45°37.5'S, 171°03'E, 420 m (1v, M.155151); head of Karitane Canyon, 45°38.5'S, 171°05.0'E, 585–530 m (1v, M.155153); Taiaroa Canyon, 45°45.4'S, 171°05'E, 549 m (2v, M.9063); Papanui Canyon, 45°46'S, 171°03'E, 660 m (1v, M.58603); Saunders Canyon, 45°55'S, 170°56'E, 421 m (1v, M.26296).

Other material examined. Off Three Kings Islands: 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (2v, M.149547); 34°10'S, 172°12'E, 252 m (1v, M.34235); SE of Great Island, 34°14.8'S, 172°13.6'E, alive, 173–178 m (2pr, 6v, M.155170); 37 km SW of Great Island, 34°20.4'S, 171°48.2'E, 440 m (1v, M.155121).

Description

Shell up to 6.50 mm long, longer than high, slightly but distinctly oblique, thin, white, no external ligament, left valve slightly smaller than right valve and seated within much of the

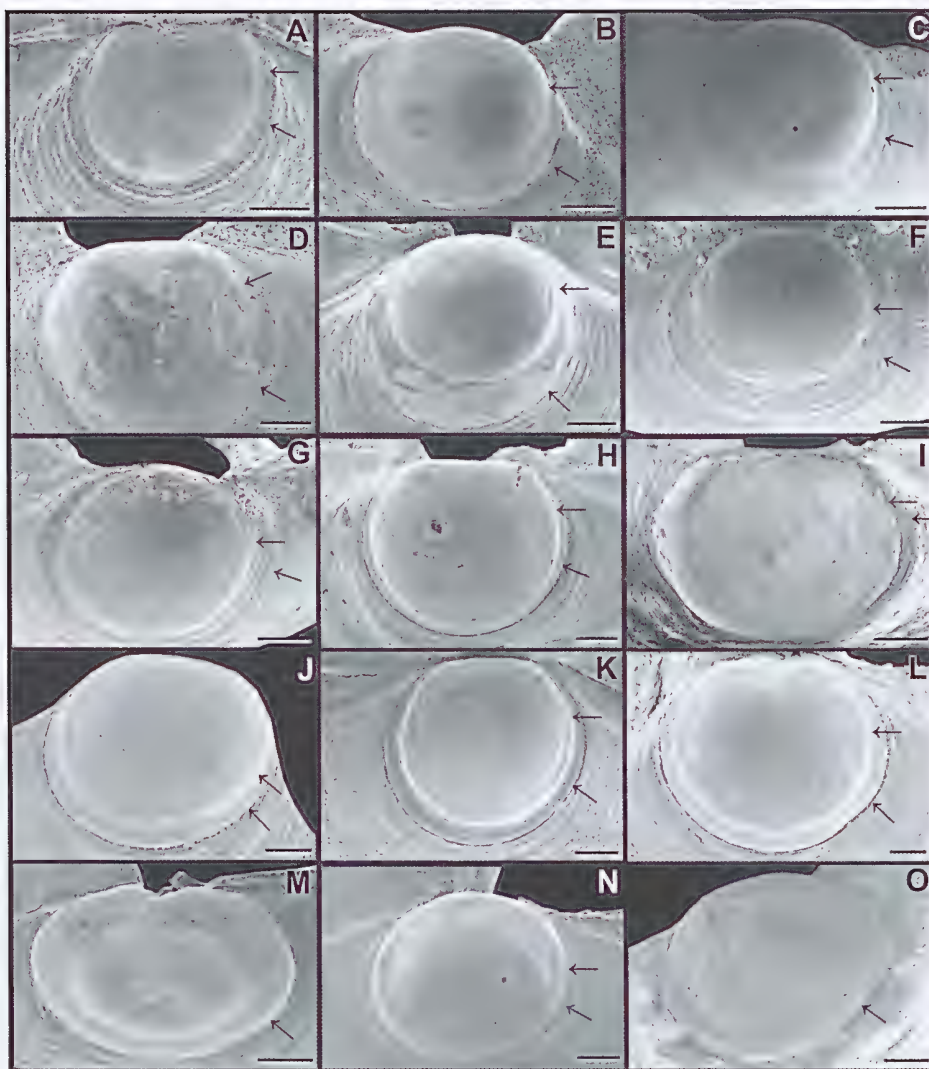


Fig. 4. Prodissococonchs of Thraciidae, Myochamidae and Cuspidariidae (prodissococonch I and II boundaries or prodissococonch boundary indicated by arrows). *A*, *Asthenothaerus maxwelli* n. sp., off Patea, 40 m (M.53531); *B*, *Barythaerus biconvexus* (Powell, 1927), off Puysegur Point, 183 m (M.7407). *C*, *Barythaerus cuneatus* (Powell, 1937), off Spirits Bay, 68 m (M.149504). *D*, *Parvithracia* (*Pseudoasthenothaerus*) *melchior* n. sp., 22 km ENE of Great Island, 200 m (M.59557). *E*, *Parvithracia* (*s. str.*) *suteri* (Finlay, 1927), North Arm, Port Pegasus, Stewart Island, 37–44 m (M.44790). *F*, *Parvithracia* (*s. str.*) *ampla* n. sp., head of Waitaki Canyon, off Oamaru, 293–256 m (M.155152); *G*, *Trigonothracia mimica* n. sp., holotype, Doubtful Sound entrance, 117–128 m (M.155019). *H–J*, *Myochama tasmanica* (Tenison Woods, 1877): *H*, Bradshaw Basin floor, Bradshaw Sound, Fiordland, 415 m (M.138438); *I*, SE of Three Kings Islands, 121 m (M.152688); *J*, Arch Pinnacle, Prince's Islands, Three Kings Islands, 40 m (M.117130). *K*, *Hunkydora novozelandica* (Reeve, 1859), North Arm, Port Pegasus, Stewart Island, 37–44 m (M.44788). *L*, *Hunkydora rakiura* n. sp., holotype, channel between Ulva Island and Bradshaw Peninsula, Paterson Inlet, Stewart Island, 33 m (M.152724). *M*, *Pseudogrippina wanganella* n. sp., Wanganella Bank summit, Norfolk Ridge, 113 m (M.152681). *N*, *Plectodon lepidus* n. sp., holotype, off E side of Mayor Island, 59–74 m (M.152682). *O*, *Plectodon pruinus* n. sp., Middlesex Bank, NW of Three Kings Islands, 98–103 m (M.152683). Scale bars: 50 μ m.

perimeter of the right valve. Prodissoconch approximately 200 μm wide, smooth; PI approximately 180 μm wide, sharply defined, more strongly inflated than PII. Beaks roundly angulate, posterior occupying approximately 40% of shell length. Posterodorsal margin straight; posterior margin broadly rounded, oblique, subtruncate, bounded above and below by tightly rounded angulations; anterodorsal margin weakly convex, anterior margin well rounded; ventral margin broadly rounded. Inflation of both valves moderate, externally convex, posterior area weakly flattened, posterodorsal margins of both valves externally bounded by sharp angulations. Right valve with prominent hinge tooth immediately below and before prodissoconch, no corresponding socket in left valve; longer, low posterior tooth separated from dorsal margin by shallow groove; long, well-defined internal shelf beside anterodorsal and posterodorsal margins that seats left valve. Resilifers oblique, narrowly ovate, anterior rim weakly elevated and undercut, lithodesma present. Adductor muscle scars and pallial line well defined; pallial sinus depth 42%–43% of adult shell length, anterior margin rounded. Exterior with irregular commarginal ridges and growth lines, dull due to exceedingly fine, granular surface texture; each valve with flattened anterodorsal and posterodorsal areas, posterior area bounded by long, low, rounded angulation, anterior area boundary rounded.

Distribution

Off Three Kings Islands, south-eastern North Island, eastern South Island, and Chatham Rise, 173–1019 m; taken alive at 238–1019 m from foraminiferal ooze and mud (Fig. 7B).

Remarks

Of the three *Parvithracia* species here recorded from the New Zealand region, *P. ampla* most closely resembles *P. suteri*, from which it differs in attaining larger size (length up to 6.50 v. 4.10 mm) and in having a longer anterior end. *Parvithracia suteri* and *P. ampla* are sympatric but asyntopic, *P. suteri* ranging into much shallower depths than *P. ampla*. I am unable to detect any differences between specimens from disjunct northern and southern populations and consider them to be conspecific.

Etymology

From the Latin *amplus* (large).

Subgenus *Pseudoasthenothaerus* Kamanev, 2002

Pseudoasthenothaerus Kamanev, 2002: 111. Type species (by original designation): *Parvithracia (Pseudoasthenothaerus) lukini* Kamanev, 2002; Recent, NW Pacific.

Parvithracia (Pseudoasthenothaerus) melchior n. sp.

Figs 4D, 5F, 6A,C

Thraciidae sp. 2 Spencer *et al.* (in press).

Material examined

Holotype. SE of Great Island, Three Kings Islands, New Zealand, 34°14.8'S, 172°13.6'E, 173–178 m, 2 Feb. 1981, RV *Tangaroa* (1v, M.155110).

Paratypes. Off Three Kings Islands: Middlesex Bank, 33°57.0'S, 171°45.4'E, 98–103 m (1v, M.149495); 37 km NE of Great Island, 33°58.0'S, 172°30.6'E, 550 m (2v, M.59550); Middlesex Bank, 33°59.9'S, 171°45.3'E, 186–196 m (3v, M.149496); Three Kings Trough, 34°00'S, 171°55'E, 805 m (2v,

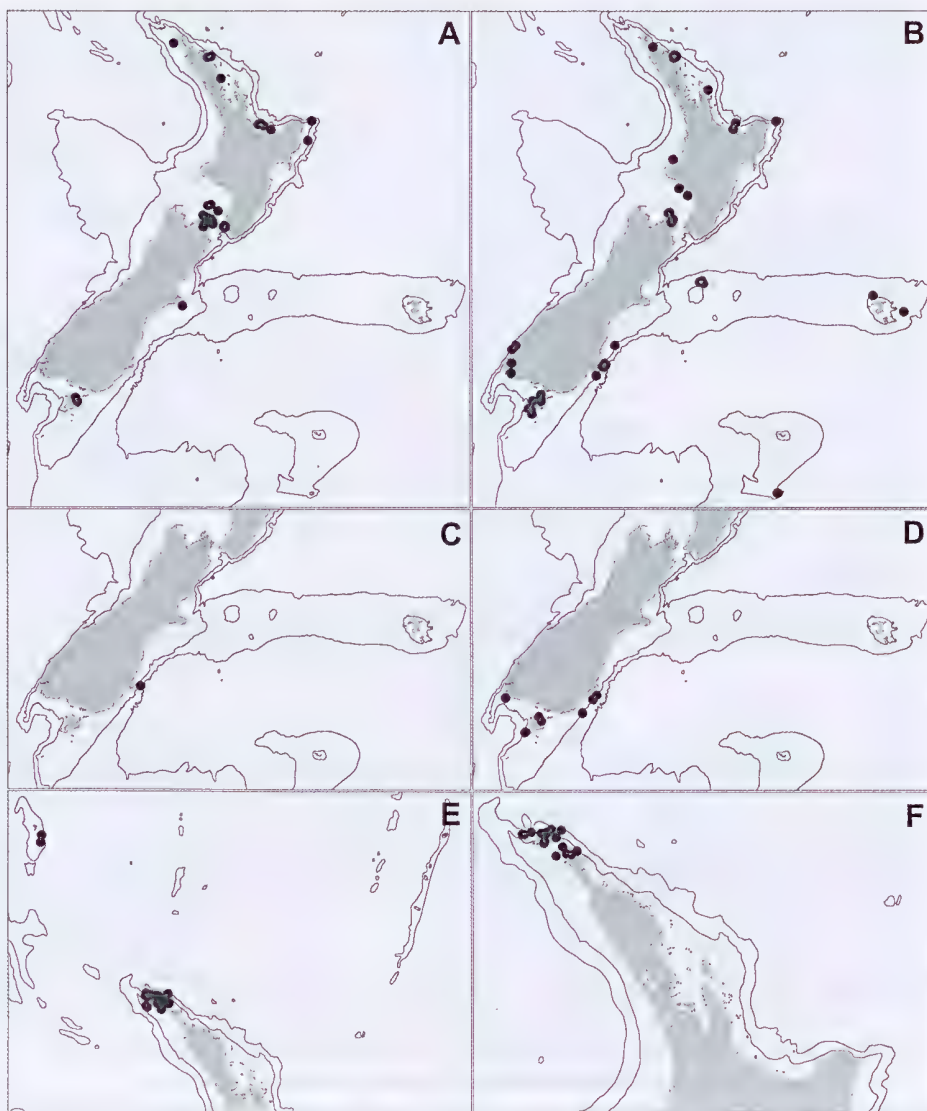


Fig. 5. Maps of the New Zealand region showing distributions of *Thracia* and *Barythaeus* species (200 and 1000 m isobaths indicated). A, *Thracia* (*Odoncincta*) *vitrea* (Hutton, 1873). B, *Asthenothaerus maxwelli* n. sp. C, *Thracia* (*Crassithracia*) *meridionalis* E. A. Smith, 1885. D, *Barythaeus biconvexus* (Powell, 1927). E, *Barythaeus cuneatus* (Powell, 1937). F, *Parvithracia* (*Pseudoasthenothaerus*) *melchior* n. sp.

M.17518); 34°01'S, 172°07'E, 622 m (2v, M.149493); Middlesex Bank, 34°01.2'S, 171°44.4'E, 206–211 m (2v, M.149494); 13 km N of Great Island, 34°01.8'S, 172°12.0'E, 508 m (1v, M.59547); Middlesex Bank, 34°02.0'S, 171°44.0'E, 246–291 m (2v, M.149499); 37 km NW of Great Island, 34°02.0'S, 171°48.4'E, 188 m (2v, M.59549); Middlesex Bank, 34°02.1'S, 171°45.8'E, 221–206 m (1v, M.149500); 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (8v, M.59557); S of Great Island, 34°14.1'S, 172°09.0'E, 192–202 m (4v, M.149492); SE of Great Island, 34°14.8'S, 172°13.6'E, 173–178 m, 2 Feb. 1981, RV *Tangaroa* (6v, M.144395); 39 km SW of Great Island, 34°17.6'S, 171°45.3'E, 427 m (3v, M.149497); 34°18.8'S, 172°18.5'E, 93–88 m (1v, M.149498); 37 km SW of Great Island, 34°20.4'S, 171°48.2'E, 440

m (3v, M.59554); 28 km S of Great Island, 34°24.0'S, 172°16.8'E, 120 m (3v, M.59553). NW of Cape Reinga, 34°14.2'S, 172°32.4'E, 100 m (4v, M.144365).

Other material examined. 29°33'S, 168°07'E, SSE of Philip Island, Norfolk Island, 143 m (5v, M.224815); 29°20'S, 168°09'E, E of Norfolk Island, 201 m (4v, M.224736).

Description

Shell up to 11.5 mm long, longer than high, slightly oblique, of moderate thickness, white, no external ligament, lithodesma not seen. Prodissoconch approximately 230 µm wide, smooth; globular PI approximately 200 µm wide. Beaks at posterior one-third to one-quarter, opisthogyrous. Posterodorsal margin straight or very weakly concave, roundly angulated to broadly rounded, subtruncate posterior margin; anterodorsal margin flat or weakly convex, anterior margin well rounded, ventral margin broadly rounded, margins smoothly merging. Inflation of both valves moderate, externally convex, posterior area flattened. Right valve with prominent hinge tooth immediately below and before prodissoconch, no corresponding socket in left valve; no trace of posterior hinge tooth and no posterodorsal groove. Resilifers oblique, narrowly ovate, anterior rim elevated and undercut. Interior glossy, not nacreous, sculptured with shallow radial grooves; adductor muscle scars and pallial line well defined; pallial sinus depth 39%–45% of adult shell length, anterior margin rounded. Exterior with well-defined posterodorsal angulations that bound concave escutcheon, no lunule; irregular commarginal ridges and growth lines; dulled by microsculpture of extremely minute, crisp, crowded granules resembling irregular paving stones (not separated by wavy radial striae).

Distribution

Off Norfolk Island and off Three Kings Islands, 88–805 m (shells only; Fig. 5F).

Remarks

Parvithracia melchior is similar to *P. ampla* in gross facies, but differs in attaining yet larger size, in having a longer anterior end and in having a more prominent tooth on the right valve. It is tentatively referred to subgenus *Pseudoasthenothaerus* because of similarity to north-west Pacific species in shape and lack of an internal groove beside the posterodorsal margin, but it differs in that the resilifer plates are not supported by pillars.

Specimens from off Norfolk Island and the Three Kings Islands have extremely similar shell morphology and appear to be conspecific.

Etymology

After Melchior, one of the Three Kings.

Parvithracia (Pseudoasthenothaerus) fragilissima n. sp.

Figs 6B,D, 7E, 21G

Material examined

Holotype. Challenger Plateau, New Zealand, 40°50.1'S, 168°14.8'E, alive, 1005–1009 m, 18 Apr. 1980, RV *Tangaroa* (pr, NZOI H-808).

Paratype. Challenger Plateau, 40°50.1'S, 168°14.8'E, alive, 1005–1009 m, 18 Apr. 1980, RV *Tangaroa* (M.158220). Off Kahurangi Point, 41°00.6'S, 169°06.0'E, alive, 914 m (2pr, M.155144; 2pr, 1v, NZOI P942). Off Westport, 41°08.1'S, 170°21.0'E, alive, 695 m (1pr, NZOI Q699). Bounty Trough, 45°21.2'S, 173°35.8'E, alive, 1386 m (1pr, NZOI S153). Saunders Canyon, off Otago Peninsula, 45°55'S, 170°56'E, 421 m (1v, M.155154).

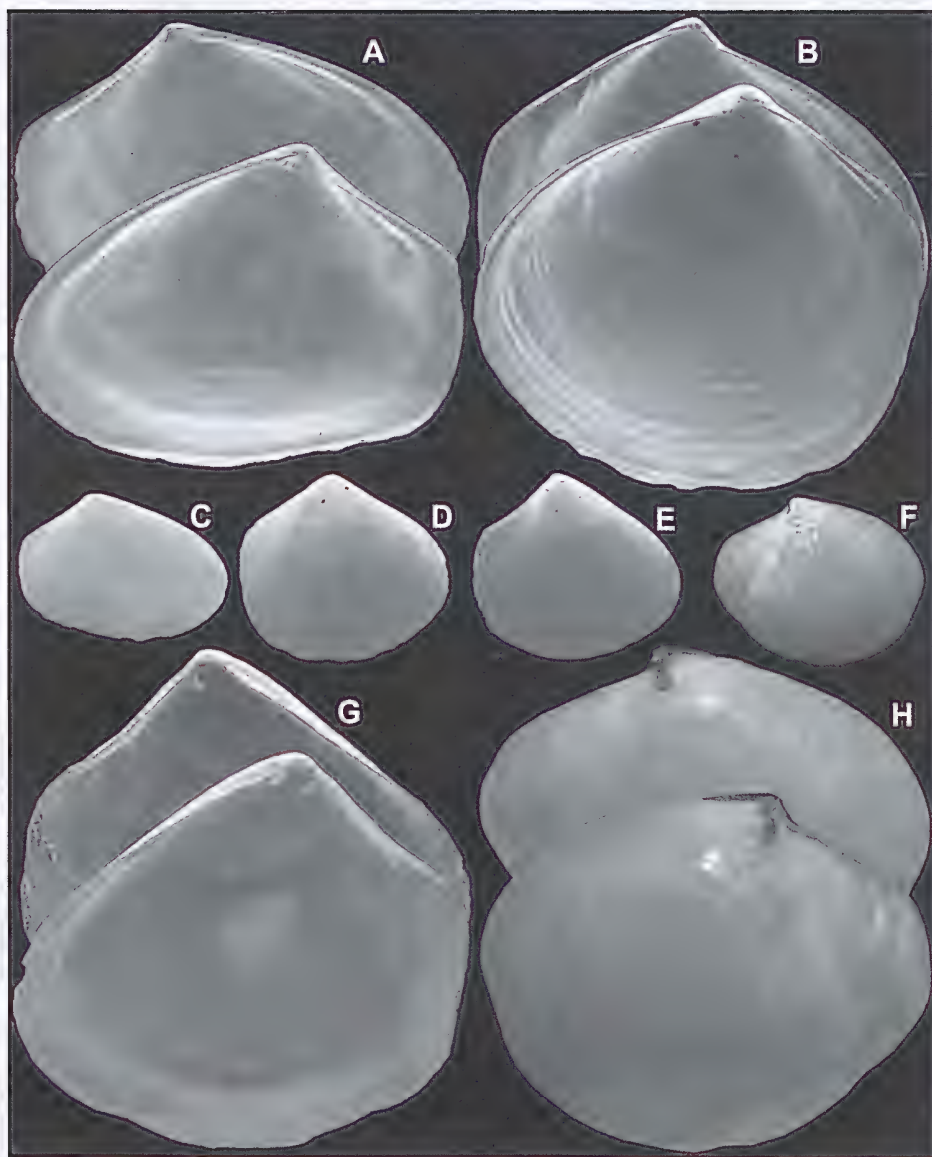


Fig. 6. Shells of *Parvithracia*, *Trigonothracia* and *Pandaloma* species. *A,C*, *Parvithracia* (*Pseudoasthenothaerus*) *melchior* n. sp.: holotype right valve (*C*, *A* lower), length 8.40 mm (M.155110) and paratype left valve (*A* upper), length 8.00 mm (M.144395), off Three Kings Islands, 200 m. *B,D*, *Parvithracia* (*Pseudoasthenothaerus*) *fragilissima* n. sp.: holotype, left (*B* upper) and right valve, length 6.70 mm, Challenger Plateau, 1005–1009 m (NZOI H-808). *E,G*, *Trigonothracia* *mimica* n. sp.: holotype, left (*G* upper) and right valve (*G* lower), length 2.05 mm (M.155019); paratype (*E*), length 2.35 mm (M.144393), Doubtful Sound entrance, 117–128 m. *F,H*, *Pandaloma* *micans* (Hedley, 1901): left (*H* upper) and right valve, length 18.0 mm, Pegasus Canyon, NE of Banks Peninsula, 622 m (M.90220).

Description

Shell up to 7.90 mm long, longer than high, very thin and fragile, white, no external ligament, rather strongly inflated, left valve slightly smaller than right valve and seated within much of the perimeter of the right valve. Prodissoconch approximately 200 μ m wide, smooth, rounded, no obvious PII (development presumably non-planktotrophic). Beaks roundly angulate, posterior occupying 43%–46% of adult shell length. Posterodorsal margin straight, tightly rounded to long, very broadly convex, slightly oblique, subtruncate, posterior margin, smoothly rounded to ventral margin; anterodorsal and ventral margins broadly convex, anterior margin well rounded. Externally posterior area shallowly concave, posterodorsal margins of both valves externally bounded by weak angulations. Right valve with weak hinge tooth immediately below and before prodissoconch, no corresponding socket in left valve; posterior tooth very weak or scarcely defined at all, separated from dorsal margin by shallow groove; narrow but well-defined internal shelf beside anterodorsal and anterodorsal margins that seats left valve. Resilifers oblique, narrowly ovate, anterior rim elevated and undercut, lithodesma present. Adductor muscle scars and pallial line well defined; pallial sinus depth 34%–38% of adult shell length, anterior margin rounded. Exterior with irregular commarginal ridges and commarginal and radial growth lines, dull but without defined microsculpture; each valve with very weak rounded angulation close to posterodorsal margin, anterodorsal area evenly rounded.

Distribution

Off north-western and south-eastern South Island, 421–1386 m; taken alive at 695–1386 m from foraminiferal ooze (Fig. 7E).

Remarks

Parvithracia fragilissima differs from other *Parvithracia* species in the New Zealand region by its thinner, more inflated shell, higher posterior truncation and, relatively, much weaker hinge teeth. It is placed in subgenus *Pseudoasthenothaerus* because of lack of a groove beside the posterodorsal margin, but it differs from north-western Pacific *Pseudoasthenothaerus* species in lacking any trace of either lunule or resilifer plate pillars.

Etymology

From the Latin *fragilis* (fragile) and *issimus* (adjectival superlative; very fragile).

Genus *Trigonothracia* Yamamoto & Habe, 1959

Trigonothracia Yamamoto & Habe, 1959: 117. Type species (by original designation): *Thracia* (*Trigonothracia*) *nomurai* Yamamoto & Habe, 1959; Recent, Japan.

***Trigonothracia mimica* n. sp.**

Figs 3E, 4G, 6E, G, 7C

Material examined

Holotype. Doubtful Sound entrance, New Zealand, 45°16'S, 166°48'E, alive, 117–128 m, 1 Jan. 1977, RV *Acheron* (pr, M.155019).

Paratypes. Doubtful Sound. Off Rangaunu Bay, 34°42.8'S, 173°14.5'E, alive, 63 m (1pr, M.155123). Off Whangaroa Bay, 34°54.0'S, 173°42.6'E, alive, 83 m (1pr, 3v, M.155122). Off Cape Brett, 35°08'S, 174°12.5'E, 80 m (2v, M.67869). Off Takau Bay, 35°10'S, 174°11'E, 80 m (5v, M.152723). W of Poor

Knights Islands, 35°32'S, 174°41'E, 121–113 m (1v, M.67871). Off Otarawairere Bay, Ohope, alive, 15 m (1pr, 2v, M.44086). N of New Plymouth, 38°40.2'S, 174°03.9'E, 88 m (2v, M.144392). NE of Kaingaroa, Chatham Islands, 43°35'S, 176°03.5'W, 220–229 m (2v, M.10863). Thompson Basin floor, Thompson Sound, 45°14.38'S, 166°58.87'E, 340–362 m (1v, M.150486). Bradshaw Basin floor, Bradshaw Sound, 45°17.3'S, 167°02.6'E, 415 m (2v, M.144394; 1v, M.138705). Seymour Basin, Malaspina Reach, Doubtful Sound: entrance, 45°16'S, 166°48'E, alive, 117–128 m, 1 Jan. 1977, RV *Acheron* (2, M.144393); 45°18.15'S, 167°00.64'E, 107 m (2v, M.147085); Seymour Basin, 45°18.27'S, 167°00.69'E, 115 m (3v, M.147248); 45°18.15'S, 167°00.64'E, alive, 107 m (1pr, M.144445). Dusky Sound: off Passage Point, 45°44.0'S, 166°43.5'E, 22–27 m (1v, M.14709); Cook Channel, 45°46.0'S, 166°43.0'E, 44 m (2v, M.144391).

Description

Shell small (length up to 3.95 mm), slightly longer than high, thin, white; periostracum extremely thin, pale cream. Prodissoconch approximately 200 µm wide, subcircular, smooth, PI approximately 180 µm wide. Right valve approximately 1% larger than left, both valves similar in thickness. Posterior length approximately 40% of shell length, beaks slightly opisthogyrous. Posterodorsal margin shallowly concave, anterodorsal margin straight, anterior margin rounded, ventral margin more broadly rounded, posterior margin strongly and slightly obliquely truncate. Prominent, slightly curved chondrophores behind well-developed lithodesma, ligament weakly developed; small, bluntly rounded tooth on right valve before lithodesma that sits against inner side of left valve (no corresponding socket). Lithodesma attachment area well defined, small, subcircular, directly below umbo. Interior glossy, not nacreous, anterior adductor scar curved, narrowly elliptical; posterior scar subtrigonal; pallial sinus depth approximately 40% of adult shell length, anterior margin rounded. Externally broadly convex; posterior area well defined, flattened; sculpture of low, irregular, rounded commarginal ridges; minute, crowded granules, considerably coarser and sharper on posterior area.

Distribution

Off NE North Island, New Plymouth, Fiordland, and Chatham Islands, 15–415 m; taken alive at 15–128 m from mud (Fig. 7C).

Remarks

Trigonothracia mimica is extremely distinctive among thraciids from the New Zealand region in its small size, subtrigonal outline, external sculpture and the conspicuous chondrophores. Although similar to the Japanese type species of *Trigonothracia* (holotype NSMT 39880; Yamamoto and Habe 1959: pl. 12, figs 9, 10; Higo *et al.* 2001: 182) in gross facies it differs in a number of details, including deeper pallial sinus, weaker inflation, more tightly rounded anterior end and a more strongly truncate posterior end, and in attaining approximately one-third the size (length 3.95 v. 10.10 mm). *Trigonothracia mimica* is remarkably similar to *Parvithracia suteri* in shape and size, but the two locally sympatric species differ markedly in hinge morphology and external sculpture.

Etymology

From the Greek *mimicus* (imitative), alluding to its resemblance to *Parvithracia suteri* in shape and size.

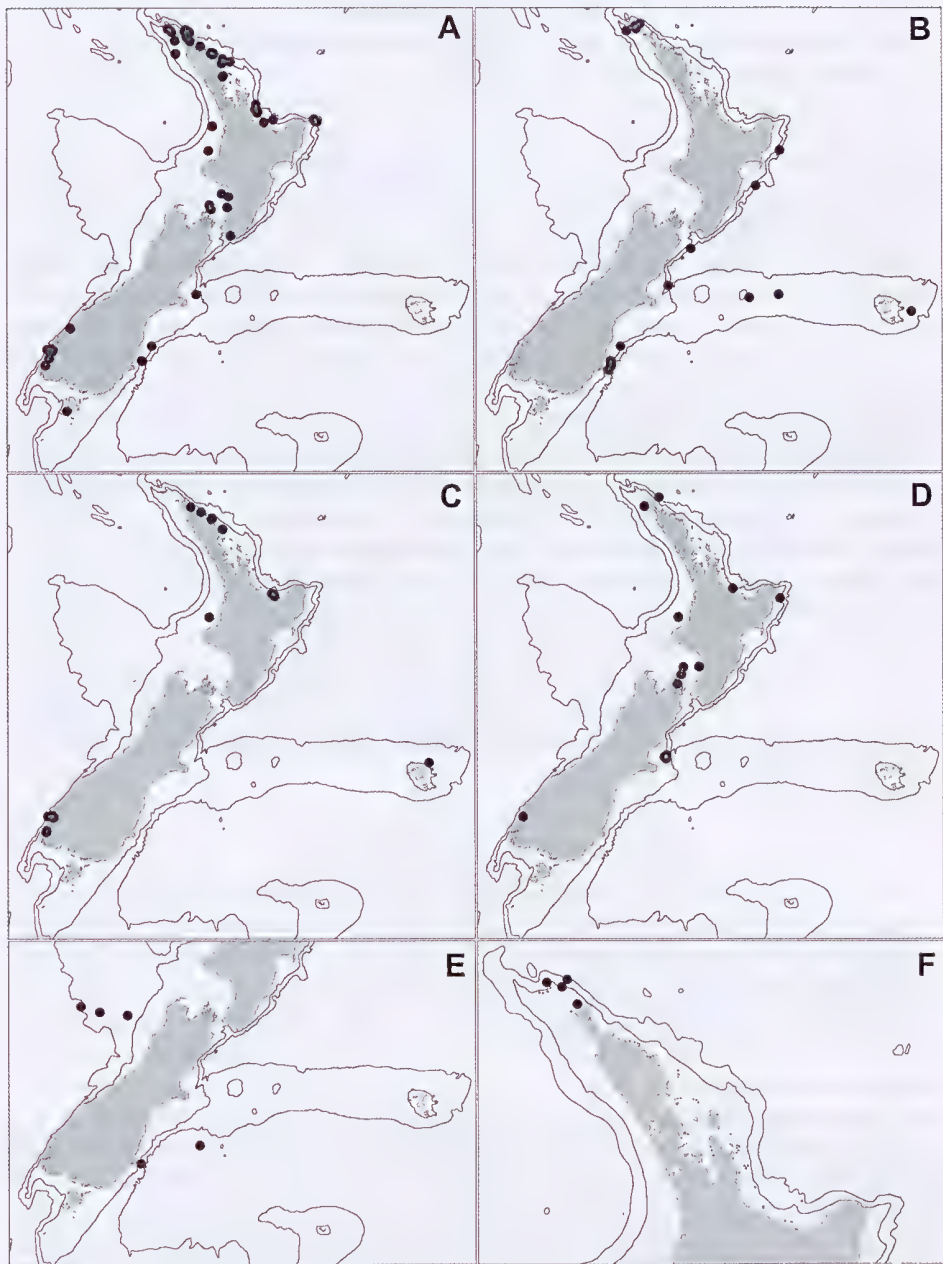


Fig. 7. Maps of the New Zealand region showing distributions of *Parvithracia*, *Trigonothracia*, *Pandaloma* and *Myadoropsis* species (200 and 1000 m isobaths indicated). A, *Parvithracia* (*s. str.*) *suteri* (Finlay, 1927). B, *Parvithracia* (*s. str.*) *ampla* n. sp. C, *Trigonothracia* *mimica* n. sp. D, *Pandaloma* *micans* (Hedley, 1901). E, *Parvithracia* (*Pseudoasthenothaerus*) *fragilissima* n. sp. F, *Myadoropsis* *wairua* n. sp.

Family PERIPLOMATIDAE Dall, 1895

Genus *Pendaloma* Iredale, 1930

Pendaloma Iredale, 1930: 387. Type species (by original designation): *Periploma micans* Hedley, 1901; Recent, New South Wales and New Zealand.

Remarks

In his review of Pacific and Indo-Pacific Periplomatidae, Bernard (1989) made no mention of *Pendaloma* and merely listed the type species among the three recognised living species of *Offadesma* Iredale, 1930. Bernard's (1989) failure to compare the type species of his new genus *Takashia* Bernard, 1989 (*Periploma plane* Ozaki, 1958; Pleistocene and Recent, Japan) with *P. micans* suggests that he may have been unaware of *Pendaloma*, because it is unclear how *Takashia* actually differs from *Pendaloma*. The type species of *Pendaloma* differs from that of *Offadesma* (*Cochlodesma angasi* Crosse & P. Fischer, 1864; Recent, Australia and New Zealand) in attaining smaller size, in being equivalved and in being subcircular rather than subovate without a distinct rostrum. Both type species differ from the type species of *Periploma* Schumacher, 1817 (*Periploma inaequalis* Schumacher, 1817 = *Corbula margaritacea* Lamarck, 1801; Recent, Atlantic and Caribbean) markedly in shape and in lacking a lithodesma at maturity. The statements of Morton (1981) and Bernard (1989) that *Offadesma angasi* lacks a lithodesma are true of adults, although, in fact, a minute lithodesma is present in juveniles (width 270 µm in an 8-mm long individual), so evidently the structure is lost following arrested development at an early stage of growth. A lithodesma is also present in *Pendaloma micans* (Fig. 1M) and retained throughout life, although, again, development is arrested in early ontogeny and the lithodesma is eventually minute relative to the chondrophores. Another possible *Pendaloma* species is *Periploma camerunensis* Cosel, 1995 (off Cameroon), which is extremely similar to *P. micans*.

Pendaloma micans (Hedley, 1901)

Figs 1M, 6F,H, 7D

Periploma micans Hedley, 1901: 25, fig. 7.

Pendaloma micans. – Iredale, 1930: 387.

Periploma (*Pendaloma*) *micans*. – Keen, 1969b: 850, fig. F26/5a.

Offadesma micans. – Bernard, 1989: 9.

Pendaloma sp. Spencer *et al.* (in press).

Material examined

Holotype. 8 km E of Sydney, New South Wales, Australia, 82 m (AMS C8960).

Other material examined. **Australia**: New South Wales, shelf between Sydney and Cronulla, alive, 60–100 m (3pr, M.219809). **New Zealand**: E of North Cape, 34°23.0'S, 173°12.6'E, 447–357 m (1v, M.144377). SW of Cape Maria van Diemen, 34°41.9'S, 172°33.5'E, alive, 103 m (1pr, M.144360). W of Plate Island, 37°39.1'S, 176°31.5'E, 64–59 m (1v, M.67585). ENE of Tokomaru Bay, 37°59.7'S, 178°40.0'E, alive, 144 m (1pr, M.59857). N of New Plymouth, 38°40.2'S, 174°03.9'E, alive, 88 m (1pr, 1v, M.144370). NW of Manawatu R. mouth, 40°22.5'S, 174°59.5'E, 86 m (1v, M.53863). NE of Stephens Island, 40°24'S, 174°17'E, alive, 110 m (1pr, M.53095). E of Stephens Island, 40°38.5'S, 174°12.0'E, 128 m (1v, M.53221). Between West Entry Point and Duffers Reef, Pelorus Sound mouth, 40°57.5'S, 174°01.5'E, alive, 29 m (1pr, M.51510). Off Greymouth, 42°04.3'S, 170°12.5'E, alive, 750 m (1pr, NZOI Q719). Pegasus Canyon, NE of Banks Peninsula: 43°20.3'S, 173°31.4'E, alive, 622 m (4pr, M.90220); 43°24'S, 173°27'E, 439–433 m (1v, M.49769); 43°24'S, 173°26'E, alive, 366–311 m (10pr, M.51017); 43°26.9'S, 173°29.5'E, alive, 505 m (1pr, M.144361). Bradshaw Basin floor, Bradshaw Sound, 45°17.3'S, 167°02.6'E, alive, 415 m (1pr, M.138381).

Description

Shell very thin and fragile, translucent white, subcircular or laterally flexed, length up to 29.5 mm, slightly longer than high, beaks opisthogyrous, valves similar, natural radial umbonal crack forming when shell approximately 4.5 mm long, posterior length approximately 38% of shell length; periostracum very thin, pale buff. Prodissoconch unknown. Posterodorsal margin straight, posterior margin subtruncate, anterodorsal margin weakly convex, ventral margin broadly convex; larger specimens typically shallowly indented anteroventrally and posteroventrally, marginal indentations coinciding with shallow radial concavities. Chondrophores large, stout, ligamental pit concave. Lithodesma before and against chondrophores, in juveniles smaller than chondrophores, although conspicuous; development arrested at an early stage of growth (probably at approximately 4.5 mm shell length, when umbonal crack begins to form) and, thus, relatively minute and inconspicuous in adults. Interior nacreous white, pallial sinus depth 39%–40% of shell length, posterior adductor scar subcircular, anterior adductor scar narrowly elliptical. Exterior dull, convex with shallow posterior and anterior radial concavities; fine, irregular, commarginal sculpture throughout, posterodorsal area typically with addition of eight to 12 fine radial threads; posterior radial concavity delineated by more or less well-defined lines, interspace of which is flat or becomes shallowly concave with increasing size; anterior radial concavity becoming apparent with increasing shell size, margins not sharply defined.

Distribution

New South Wales. North and South Islands, New Zealand, living in mud at 29–750 m (Fig. 7D).

Remarks

Compared with *Offadesma angasi* (Crosse & P. Fisher, 1864), the only other Recent periplomatid known from the New Zealand region, *Pendaloma micans*, differs principally in attaining smaller size (length of largest specimen seen 29.5 v. 102.5 mm) and in having a deeper, more broadly rounded pallial sinus, a well-defined band that curves posteriorly from the umbo to the posteroventral margin and fine collabral wrinkles and, typically, radial threads instead of minute but distinct, sharp granules on the posterodorsal area. Whereas *O. micans* lives at 29–750 m, *O. angasi* lives at low tide level to probably as deep as 64 m (very fresh paired juvenile from floor of Seymour Basin, Fiordland, New Zealand and New South Wales specimens are indistinguishable in shell morphology).

Other Anomalodesmata common to Australia and New Zealand are *Offadesma angasi*, *Myochama tasmanica* (Tenison Woods, 1877), *Cleidochaerus albidus* (Lamarck, 1819), *Spinospella ericia* (Hedley, 1911) and, possibly, *Poromya australis* E. A. Smith, 1885 (recorded as *P. undosa* Hedley and Petterd, 1906 by Dell (1995); see Krylova (2001)). Genetic interchange between these disjunct populations is presumably maintained by larval stages of sufficient duration for planktotrophic larvae to reach New Zealand from Australia in eastward-moving water masses. However, genetic interchange may be intermittent and the rate of evolution in these taxa may simply be slow.

Superfamily **PANDOROIDEA** Rafinesque, 1815Family **MYOCHAMIDAE** Bronn, 1862Genus *Myadoropsis* Habe, 1960

Myadoropsis Habe, 1960: 293. Type species (by original designation): *Myadora transmontana* Yokoyama, 1922; Recent, Japan.

Myadoropsis wairua n. sp.

Figs 3*F*, 7*F*, 8*A*, *D*

Myadoropsis sp. Spencer *et al.* (in press).

Material examined

Holotype. N of Three Kings Islands, New Zealand, 34°01'S, 172°07'E, 622 m, 18 Feb. 1974, RV *Acheron* (left v, M.152686).

Paratypes. 37 km NE of Great Island, Three Kings Islands, 33°58.0'S, 172°30.6'E, 550 m (2v, M.149507). N of Three Kings Islands, 34°01'S, 172°07'E, 622 m, (3v, M.34999). 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (1v, M.93352). Off Spirits Bay, 34°21.60'S, 172°43.19'E, 48 m (2v, M.149506).

Description

Shell up to 5.10 mm long, translucent white, massively secondarily thickened internally, strongly inequilateral, both valves modestly inflated, right valve slightly less inflated than left, 1.62–1.64× longer than high; umbones strongly opisthogyrous, at posterior one-sixth to one-quarter; concave escutcheon bounded by angulation. Prodissoconch approximately 270 µm wide, almost circular, convex, surface etched but apparently naturally smooth. Dissoconch anterodorsal and ventral margins very broadly rounded, posterodorsal margin concave, anterior margin well rounded, posterior margin obliquely subtruncate. Hinge plate extremely thick, anterior and posterior parts separated by deep, oblique ligamental groove; right valve with two strong, although poorly delineated, divergent teeth, antero- and posterodorsal margins grooved to interlock with corresponding, sharp, elevated margins of left valve. Pallial sinus depth 34%–36% of shell length. Adductor and anterior pedal retractor muscle scars well defined. Exterior typically with strong, rounded commarginal ridges, strongest over posterior half, obsolete in some specimens. Periostracum set with minute, crowded, commarginally elongate, hexagonal calcareous prisms that form the outermost shell layer.

Distribution

Off Three Kings Islands and Spirits Bay, 48–550 m from comminuted bryozoan/shell substrata (shells only; Fig. 7*F*).

Remarks

Myadoropsis wairua differs from other nominal species of *Myadoropsis* principally in having a dorsoventrally lower posterior rostrum. Congeners are *M. elongata* (May, 1915) from south-eastern Australia and the Japanese species *M. transmontana* (Yokoyama, 1922), *M. dissimilis* Habe, 1960 and *M. brevispinosa* Habe, 1962. *Myadoropsis wairua* superficially resembles the thraciids *Barythaerus biconvexus* (Powell, 1927) and *B. cuneatus* (Powell, 1937; see above), but is immediately separable by the much heavier hinge area, the lack of a well-defined hinge tooth on the right valve and the distinctive microsculpture.

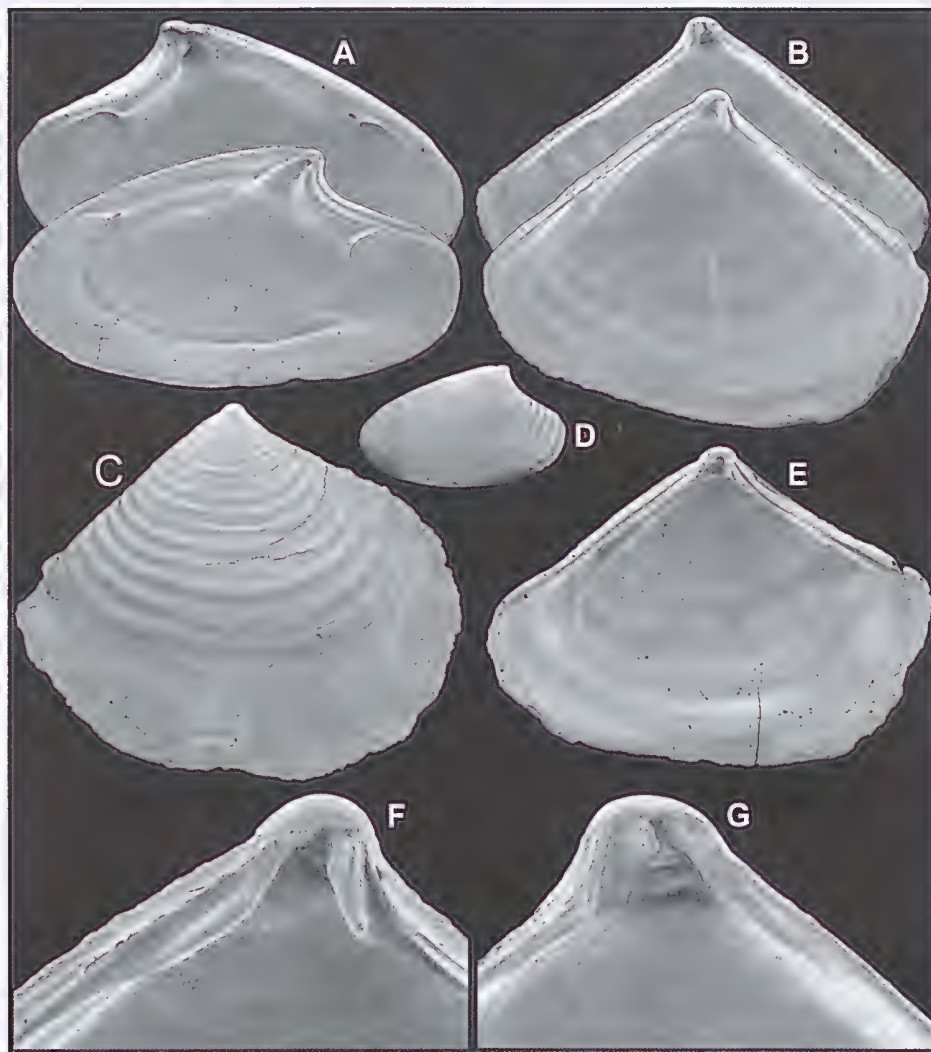


Fig. 8. Shells of *Myadoropsis* and *Myochama* species. *A,D*, *Myadoropsis wairua* n. sp.: holotype, left valve (*A* upper, *D*), length 4.70 mm, N of Three Kings Islands, 622 m (M.152686); paratype, right valve (*A* lower), length 4.40 mm, 37 km NE of Great Island, Three Kings Islands, 550 m (M.149507). *B,C,E-G*, *Myochama tasmanica* (Tenison Woods, 1877): *B,F,G*, juvenile, precementation, left (*B* upper, *G*) and right valve, length 2.90 mm, SE of Three Kings Islands, 121 m (M.152688); *C*, juvenile, early cemented stage, left valve, length 4.30 mm, Arch Pinnacle, Prince's Islands, Three Kings Islands, 40 m (M.117130). *E*, juvenile, precementation, right valve, length 2.55 mm, Bradshaw Basin floor, Bradshaw Sound, Fiordland, 415 m (M.138438).

Etymology

From the Maori *wairua* (spirit), alluding to departure place of spirits in the vicinity of the type locality.

Genus *Myochama* Stutchbury, 1830

Myochama Stutchbury, 1830: 96. Type species (by monotypy): *Myochama anomioides* Stutchbury, 1830; Recent, Australia.

Myochama tasmanica (Tenison Woods, 1877)

Figs 3G, 4H–J, 8B,C,E–G, 11A

Gouldia tasmanica Tenison Woods, 1877: 158.

Myochama woodsii Petterd, 1884: 145.

Myochama tasmanica. – Tate & May, 1901: 461, fig. 13; May, 1921: 14; May, 1923: pl. 5, fig. 11; Cotton & Godfrey, 1938: 140, fig. 135; Cotton, 1961: 149, fig. 140; Macpherson, 1958: 9, pl. 5, fig. 11; Powell, 1974: 197, figs 1–8; Powell, 1979: 432, text fig. 115; Lamprell & Healy, 1998: 216, fig. 632.

Material examined

Syntypes of Myochama tasmanica: Long Bay, Tasmania; Tasmanian Museum, Hobart (2v, E63/7404).

Myochama woodsii: repository of type material unknown.

Other material examined. Off Three Kings Islands: Middlesex Bank, 33°57.0'S, 171°45.4'E, 98–103 m, 31 Jan. 1981 (1v, M.152690); King Bank, 33°57.0'S, 172°19.0'E, 128 m, 1 Feb. 1981 (3v, M.152689); King Bank, 33°57.4'S, 172°19.4'E, 128–123 m, 1 Feb. 1981 (1v, M.152691); Middlesex Bank, 33°59.8'S, 171°46.8'E, 143–163 m, 31 Jan. 1981 (1v, M.152687); off North-east Island, 34°08.5'S, 172°11'E, 102 m, 18 Feb. 1974 (1v, M.34578); E of Great Island, 34°10.5'S, 172°11.4'E, 153 m, 1 Feb. 1981 (1v, M.152692); Arch Pinnacle, Princes Rocks, 34°10.5'S, 172°03.0'E, 38 m, 1 Feb. 1983 (3v, M.154165); off Arch Pinnacle, 40 m, 10 Mar. 1983 (1v, M.117130); off West Island, *Elingamite* wreck, 34°11'S, 172°03'E, 37 m, 16 Mar. 1981 (3v, M.152693); 34°20.2'S, 172°21.8'E, 121 m, 2 Feb. 1981 (2pr, M.152688). Off Spirits Bay: 34°23.87'S, 172°45.62'E, 30 m, 24 Jan. 1999 (1v, M.153099); 34°24.31'S, 172°49.95'E, 29 m, 24 Jan. 1999 (2pr, 1v, M.153081). Parengarenga Harbour: 6–7 m (6v, M.117599); off Dog Island, 1979 (1pr, M.155465). Immediately outside Whangaroa Harbour entrance, 35°00.35'S, 173°45.7'E, 25 m, 26 Jan. 1981 (3v, M.158226). Bay of Islands: 35°11.5'S, 174°15.5'E, 54–58 m, 9 Feb. 1976 (1v, M.131122); Deepwater Cove entrance, 35°12'S, 174°18'E, 46 m, 10 Dec. 1973 (1v, M.41698). Off Ngairo Rock, Poor Knights Islands, 35°29.5'S, 174°44.0'E, alive, 22 m, 16 Apr. 1989 (1pr, 1v, M.158229). Bradshaw Basin floor, Bradshaw Sound, 45°17.3'S, 167°02.6'E, 415 m, 31 May 1997 (1v, M.138438). Off Taiaroa Head: head of Karitane Canyon, 45°38.5'S, 171°05.0'E, 585–530 m, 19 Mar. 1976 (1v, M.51115); 45°50.85'S, 171°01.71'E, alive, 555–604 m, 4 Jun. 1992 (2pr, 13v, M.130631); Saunders Canyon, 45°55'S, 170°56'E, 549 m, 2 Mar. 1954 (1v, M.9121). Stewart Island: off South Cape, 73–91 m (1v, M.63805); off Poutama Island, Big South Cape Island, 47°16'S, 167°23'E, 55 m, Jun. 1955 (1v, M.63787).

Description

(Supplemental to that of Powell, 1974). Prodissoconch approximately 250 µm wide, smooth; PI approximately 230 µm wide, globular. Periostracum set with minute, crowded, commarginally elongate, hexagonal calcareous prisms that form outermost shell layer. Following shell length of approximately 3 mm, when right valve becomes cemented to substratum, periostracum becoming fully calcified and rigid (rather than flexible as before) and essentially 'draped' from rib summit to summit of the commarginal ribs, so covering interstitial voids.

Distribution

South Australia, Tasmania and New Zealand: Three Kings Islands, Parengarenga Harbour, Matai Bay (Gardner 1976), Bay of Islands, Poor Knights Islands, East Otago, Fiordland and Stewart Island, living at 6–604 m cemented by right valve to shells (Fig. 11A).

Remarks

The original description of *M. tasmanica* is based on juveniles in the pre-attachment stage (Tenison Woods, 1877). Cotton and Godfrey (1938: fig. 135) illustrated a juvenile and

provided an abridged version of the original description (both copied by Cotton (1961)), although, from the given dimensions (13×13 mm), it is clear that they were well aware that the type specimens were immature. Lamprell and Healy (1998) illustrated an adult, but their description seems to have been derived from their reproduction of the illustration of Cotton and Godfrey (1938: fig. 135). Both juvenile and adult Tasmanian specimens were illustrated by May (1923: pl. 5, fig. 11; reproduced by Macpherson (1958)). *Myochama tasmanica* differs from *M. anomioides* in attaining smaller size (width up to 18 v. 25 mm), in having radial grooves on the interior surface, in the considerably weaker inflation of the left (free) valve and in having commarginal rather than radial sculpture on the the left valve after settlement.

The prodissococonch of *Myochama tasmanica* has an extremely narrow PII stage (Fig. 4H–J), suggesting that larval development is non-planktotrophic, presumably lecithotrophic. I am unable to detect any differences between prodissococonchs of Australian and New Zealand specimens. Although development is apparently non-planktotrophic, the strongly disjunct distribution off the northern North Island and the southern South Island of New Zealand suggests initial origin from eastern Australia via north-eastward and south-eastward moving parts of the East Australian Current. The fact that *M. tasmanica* occurs at considerable depth off southern New Zealand, with a record there dating back to 1954, indicates that it is neither a 'warm water' species nor a recent invader, as findings in Parengarenga Harbour suggested to Powell (1976).

Shell structure, anatomy, cementation and substratum preference in *Myochama ostreoides* has been discussed by Harper and Morton (2000).

Genus *Hunkydora* Fleming, 1948

Hunkydora Fleming, 1948: 80. Type species (by original designation): *Thracia transenna* Suter, 1913 = *T. novozelandica* Reeve, 1859; Recent, New Zealand.

Remarks

Fleming (1948) correctly referred *Hunkydora* to Myochamidae on the basis of characteristically myochamid exterior shell microsculpture and hinge morphology and clearly differentiated it from other myochamid genera. Keen (1969b) retained the genus in Myochamidae. Powell's (1974, 1976, 1979) subsequent placement of *Hunkydora* in Thraciidae (as a subgenus of *Thracia*) was due to confusion of *H. novozelandica* with the thraciids *Asthenothaerus maxwelli* n. sp., and *Thracia vitrea* (Hutton, 1873) (see above). Morton (1977) judged that *Hunkydora* belonged in Thraciidae from shell morphology of a specimen he identified as '*Hunkydora australica* (Fleming, 1951)', although it is unclear whether this was *H. novozelandica*, *T. vitrea* or, seemingly most likely (because it is the most common of the three species in collections), *A. maxwelli*. *Hunkydora* species certainly are strikingly similar to several thraciids in gross shell facies, but are separable by the commarginally elongate, hexagonal, calcareous periostracal prisms, which, characteristically of myochamids, are arranged in sharply defined, irregular, wavy radial lines (unlike the superficially similar microsculpture of some thraciids, which comprise rounded elongate granules that are not grouped in radial lines; personal observation). Moreover, the left valve is considerably less inflated than the right valve, as in the majority of myochamids (i.e. markedly inequivalve), but, unlike thraciids, in which the left valve is, at most, only slightly less inflated than the right (note that myochamids of the genus *Myadoropsis* species are equivalve; see above). The outer shell layer on the interior is nacreous, as is characteristic of myochamids, although a few undoubted thraciids also have a nacreous layer (see above).

Hunkydora novozelandica (Reeve, 1859)

Figs 1F, 4K, 9A–F, 11B, 21H

Thracia novozelandica Reeve, 1859: 12, pl. 3, fig. 19.*Thracia novaezeelandiae* [sic]. – Martens, 1873: 41.*Thracia novaezeelandiae* [sic]. – Hutton, 1873a: 61; Hutton, 1880: 136.*Myadora australica*. – Smith, 1885: 67 (in part not Reeve, 1859).*Thracia transenna* Suter, 1913: 1023, pl. 55, figs 9, a.*Eximiothracia transenna*. – Finlay, 1926: 474.*Hunkydora transenna*. – Fleming, 1948: 80, pl. 4, fig. 8, pl. 7, figs 6–9.*Hunkydora australica novozelandica*. – Fleming, 1951: 135, pl. 20, figs 3–5.*Thracia vitrea*. – Dell, 1956: 41 (in part + *Asthenothaerus maxwelli*); Powell, 1957: 84 (in part: pl. 11, fig. 24 = *A. maxwelli*); Powell, 1962: 125 (in part: pl. 11, fig. 24 = *A. maxwelli*).*Myadora* (*Hunkydora*) *novozelandica*. – Keen, 1969b: 847, figs 4a–c.*Thracia* (*Hunkydora*) *australica novozelandica*. – Powell, 1976: 131 (in part = *Thracia vitrea* + *A. maxwelli* (pl. 18, fig. 24)); Powell, 1979: 433, pl. 79, fig. 9 only (in part = *T. vitrea* + *A. maxwelli* (pl. 79, figs 6, 7)).NOT *Thracia* (*Hunkydora*) *australica novozelandica*. – Powell, 1974: 200, figs 13, 14 (= *A. maxwelli*).*Material examined**Lectotype of Thracia novozelandica* (Fleming 1951). ‘New Zealand’, type locality here designated as Port Pegasus, Stewart Island (BMNH 20010411/1).*Paralectotype of Thracia novozelandica*. Same data as lectotype (BMNH 20010411/2).*Lectotype of Thracia transenna* (Borcham 1959). Port Pegasus, Stewart Island, 22 m (NZGS TM 404)*Paralectotype of Thracia transenna*. Same data as lectotype (1v, M.10984).

Other material examined. Fossil: large bend on Burma Road, between Whakatane and Ohope, brown siltstone, Late Pleistocene (Castlecliffian) (2v, M.96478); Languard Bluff, Wanganui (Castlecliffian) (2v, M.15757). Recent: off Three Kings Islands: King Bank, 33°57.0'S, 172°19.0'E, 128 m (4v, M.150900); King Bank, 33°57.4'S, 172°19.4'E, 128–123 m (2v, M.150875); Middlesex Bank, 33°59.8'S, 171°46.8'E, 143–163 m (1v, M.150883); 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (1v, M.150881); E of Great Island, 34°10.5'S, 172°11.4'E, 153 m (1v, M.150885); S of Great Island, 34°14.1'S, 172°09.0'E, 192–202 m (2v, M.150876). NW of Cape Reinga, 34°14.2'S, 172°32.4'E, 100 m (2v, M.150884); off Spirits Bay, 34°17.38'S, 172°44.00'E, 85 m (2v, M.148268); off Spirits Bay, 34°18.36'S, 172°49.39'E, 68 m (1v, M.148258); N of North Cape, 34°20.0'S, 173°06.6'E, 163–168 m (2v, M.150893); SE of Three Kings Islands, 34°20.2'S, 172°21.8'E, alive, 121 m (2pr, 1v, M.150896). N of Cape Reinga, 34°21'S, 172°37'E, alive, 88 m (1pr, M.36018). NW of Cape Reinga, 34°22.8'S, 172°24.6'E, alive, 121 m (1pr, 1v, M.150890). Great Exhibition Bay: 34°33.4'S, 173°04.8'E, 63 m (4v, M.113152); 34°33.8'S, 173°04.6'E, 63–65 m (1v, M.150897). SW of Cape Maria van Diemen, 34°41.9'S, 172°33.5'E, 103 m (5v, M.150891). Off Doubtless Bay, 34°56.0'S, 173°34.0'E, 47 m (12v, M.25817). Bay in Stephenson's Island, opposite Whangaroa Heads, 34°58'S, 173°47'E, 22–24 m (1v, M.41351; 2v, M.41553); Whangaroa Harbour entrance, main channel, 35°02'S, 173°45'E, 13 m (2pr, M.42013). Whangaroa Harbour, centre of Kaouou Bay, 35°02'S, 173°45'E, 13 m (2v, M.41766). Off Cape Brett, 35°08'S, 174°12.5'E, alive, 80 m (1pr, 6v, M.35731). Bay of Islands: NE of Ninepin Rock, 35°08.8'S, 174°10.9'E, 79 m (7v, M.28471); NE of Ninepin Rock, 35°08.8'S, 174°10.3'E, 75 m (18v, 30720); between Hope Passage and Twin Rocks, 35°10'S, 174°18'E, 46–55 m (2v, M.41260); off Takau Bay, 35°10'S, 174°11'E, 80 m (6v, M.43594); off Twin Rocks, 35°10'S, 174°18'E, 46–73 m (3v, M.42149); off Takau Bay, 35°10.5'S, 174°10'E, 37 m (3v, M.43485); 35°10.5'S, 174°19.3'E, 36–53 m (1v, M.95672); 35°10.6'S, 174°15.4'E, 67–73 m (3v, M.96009); 35°10.6'S, 174°19.6'E, 20–27 m (1v, M.95589); 35°11.2'S, 174°16.7'E, 58–64 m (2v, M.96082); off island at entrance to Deep Water Cove, 35°11.9'S, 174°17.1'E, alive, 47–49 m (1pr, 1v, M.95704); Deepwater Cove entrance, 35°12'S, 174°18'E, 46 m (3v, M.41714); Deepwater Cove entrance, 35°12'S, 174°18'E, 33–46 m (1v, M.41477); between Hope Passage and Twin Rocks, 35°12'S, 174°18'E, 37 m and 37–40 m (1v, M.41395; 1v, M.41289); W of Motuwheke Island, 35°12.3'S, 174°16.4'E, 43 m (1v, M.96057); Waewaetorea Passage, 35°12.5'S, 174°12.9'E, 4 m (1v, M.39671); 35°12.6'S, 174°16.4'E, 32–40 m (2v, M.95877); Bamboo Bay, Moturua Island, 35°13.9'S, 174°11.3'E, 4–6 m (1v, M.44478; 1v, M.40823); Rawhiti Bay, 35°14.0'S, 174°15.3'E, 2–4 m (1v, M.40801); 35°15.4'S, 174°11.5'E, near Knob Point, 4 m (1v, M.44640); Orakawa Bay, 35°15.3'S, 174°11.8'E, 4 m (1v, M.44451); Western Manawara Bay, 35°16.0'S, 174°11.5'E, 6–7 m (1v, M.44756). Off Poor Knights Islands: 35°22'S, 174°43'E, 146 m (4v, M.35105); 35°29'S, 174°43.5'E, 110

m (1v, M.35198); 35°32'S, 174°41'E, 121–113 m (6v, M.35807). Whangarei Harbour, off point SW of Munro Bay, 35°47.8'S, 174°28.9'E, alive, 7–10 m (1pr, M.152673); Castle Rock, Taurikura Bay, Whangarei Heads, 6–8 m (1v, M.43265); Taurikura Bay (2pr, 4v, M.18353). S of Lady Alice Island, Hen and Chicken Islands, 35°55.0'S, 174°43.5'E, 47–55 m (1v, M.150880). Off Hen Island, 36°00.5'S, 174°43'E, 59 m (6v, M.43789). SE of Te Arai Point, Mangawhai, Northland, 36°10.5'S, 174°42.0'E, 38–40 m, sand and shell suction dredged for beach replenishment at Mission Bay, Auckland (6v, M.138169; 3v, M.130830). NE of Takatu Point, 51–57 m (1v, M.21674); off Cuvier Island, 49–73 m (1v, M.3461). Omaha Bay: 36°20.41'S, 174°49.38'E, alive, 17 m (1pr, M.136165); 36°21.38'S, 174°51.03'E, alive, 28 m (1pr, M.136164). N of Aldermen Islands, 36°47.5'S, 176°00.0'E, 108–113 m (1v, M.150898). Off E side of Mayor Island, 37°18.9'S, 176°16.2'E, 59–74 m (1v, M.65726). Off White Island: 37°30.4'S, 177°09.7'E, 83–92 m (1v, M.150892); 37°30.6'S, 177°09.7'E, 73–59 m (1v, M.150886). Rungapapa Knoll, W of White Island, 37°33.5'S, 176°59.4'E, 198–188 m (2v, M.59995). Ranfurly Bank, East Cape: 37°32.8'S, 178°48.7'E, 94 m (6v, M.60708); 37°33.1'S, 178°49.5'E, alive, 94–89 m (4pr, 10v, M.71765); 37°33.4'S, 178°48.3'E, alive, 106–103 m (1pr, 3v, M.71784); 37°35.8'S, 178°47.0'E, 118–119 m (1v, M.150889); 37°38.5'S, 178°56.4'E, alive, 153–143 m (1pr, 3v, M.150899). Off Plate Island, 37°39.4'S, 176°34.4'E, 82 m (6v, M.67685). Between Motuhora and White Islands, 37°40.2'S, 178°53.6'E, 117 m (1v, M.112426). W of Plate Island, 37°39.1'S, 176°31.5'E, alive, 64–59 m (1pr, 9v, M.79735). NNE of Hicks Bay, 37°32'S, 178°25'E, alive, 108–134 m (1pr, M.16936). SE of Plate Island, 37°43.4'S, 176°38.5'E, 59 m (1v, M.65256). N of Motuhora Island, 37°45.8'S, 177°00.8'E, 72–84 m (1v, M.60616); ENE of Tolaga Bay, 38°15.2'S, 178°38.6'E, alive, 139 m (1pr, M.59803). S of Patea, 39°56'S, 174°26'E, 40 m (1v, M.95574). S of Waverley, 40°10'S, 174°40'E, 77–82 m (3v, M.50644). W of Rangitikei R. mouth, 40°16'S, 174°58.5'E, 75 m (2v, M.53363). NW of Manawatu R. mouth, 40°22.5'S, 174°59.5'E, alive, 86 m (2pr, M.53881). NE of Stephens Island, 40°33'S, 174°07'E, 132 m (2v, M.52998). Off shelf of flats inside Fairwell Spit, 40°36.5'S, 173°00.5'E, 26–24 m (2v, M.50022). N of Kapiti Island, 40°38'S, 174°54.5'E, 91 m (2v, M.52935). E of Stephens Island: 40°38.5'S, 174°12.0'E, 128 m (3v, M.53214); 40°42'S, 174°10.6'E, 106 m (1v, M.12929). Main channel, Port Hardy, D'Urville Island, 40°46.0'S, 173°52.5'E, alive, 18 m (1pr, 4v, M.58956). W of Kapiti Island, 40°46.2'S, 174°27.0'E, 137 m (1v, M.12927). N of Alligator Head and E of Rangitoto Islands, Marlborough Sounds, 40°47'S, 174°10.5'E, 73 m (6v, M.54089). E of D'Urville Island, Cook Strait, 40°48.6'S, 174°06.6'E, 60 m (1v, M.150888). Kapiti Channel, 40°51'S, 174°58'E, 64 m (8v, M.52233). W of Kapiti Island, 40°52.6'S, 174°49.5'E, 137 m (4v, M.150879). Between West Entry Point and Duffers Reef, Pelorus Sound mouth, 40°57.5'S, 174°01.5'E, 29 m (1v, M.51517). Off White Rocks, Queen Charlotte Sound, 41°04.3'S, 174°22.5'E, 46 m (1v, M.150882). Pegasus Canyon wall, NE of Banks Peninsula, 43°25.0'S, 173°26.0'E, alive, 329–183 m (1pr, M.71298). Off Oamaru: 110 m (1v, M.11361); 55–88 m (7v, M.111171); head of Waitaki Canyon, 45°10'S, 171°30'E, 293–256 m (12v, M.51261). Open Cove, Thompson Sound, 45°10.5'S, 167°05.0'E, 37 m (1v, M.84086). Doubtful Sound: entrance, 45°16'S, 166°48'E, 117–128 m (3v, M.144398); 0.8 km SW of Hare's Ears, 45°17.2'S, 166°49.3'E, 146 m (10v, M.58770); Kellard Basin floor, 45°21.30'S, 167°03.36'E, alive, 376 m (1pr, M.138600). Dusky Sound, 55 m (1v, M.15935). Off Taiaroa Heads: 45°36.55'S, 170°51.88'E, 41–59 m (2v, M.112307); Karitane Canyon, 45°37.5'S, 171°03'E, 420 m (1v, M.45553); Karitane Canyon, 45°38.5'S, 171°01'E, 200 m (1v, M.45434); 45°41.85'S, 170°58.72'E, 100–97 m (1v, M.112332); Taiaroa Canyon, 45°45.4'S, 171°05'E, alive, 549 m (1pr, 2v, M.9040); 45°50'S, 170°56'E, 105 m (9v, M.45376); Papanui Canyon, 45°51'S, 171°00'E, 348–220 m (1v, M.94878). Kisbee Bay, Preservation Inlet, 46°07.1'S, 166°44.0'E, 5–10 m (1v, M.59271). Off Taieri, S of Dunedin, 46°09.0'S, 170°27.0'E, 60 m (3v, M.66937); 46°15.0'S, 170°29.0'E, 91 m (4v, 66171). Stewart Island: Easy Harbour, 47°09'S, 167°34'E, 7–20 m (1v, M.26518); North Arm, Port Pegasus, 47°11'S, 167°41'E, alive, 37–44 m (2pr, 2v, M.44788); North Arm, 47°11'S, 167°41'E, 40–46 m (2v, M.26619).

Description

Shell up to 42 mm long, of moderate thickness; left valve smaller than right valve although more elongate, approximately half as inflated, lying within its perimeter; interior nacreous white, margins opaque white, some specimens with a yellowish patch near centre of valve. Prodissoconch 220–250 µm wide; PI approximately 200 µm wide, minutely pitted, circular, strongly inflated. Dissoconch anterodorsal margin flat or broadly convex, posterodorsal margin broadly concave, anterior margin tightly rounded, ventral margin broadly rounded; right valve posterior margin set off from posterodorsal margin by angulation, flat, weakly convex or shallowly concave, markedly arched relative to valve plane; left valve posterior margin subtruncate, almost vertical, more or less flat, smoothly merging with posterodorsal

margin, plane flexed to contact corresponding arched part of right valve. Exterior: narrow, flat or shallowly concave anterodorsal area of left valve defined by angulation, sharp throughout or progressively weakening; ovate, shallowly concave escutcheon bounded by angulation on left valve only, margin on right valve tightly rounded; posterior one-quarter of left valve distinctly flattened, elsewhere broadly and rather evenly convex; posterior one-quarter of right valve defined by low rounded radial swelling, in most specimens followed posteriorly by shallow radial concavity (lacking in few specimens), then rounded radial swelling that extends to escutcheon margin, elsewhere broadly convex. Right valve hinge with small tooth at anterior extremity of posterodorsal margin, otherwise edentulous, anterior and posterior parts separated by narrow V-shaped space for lithodesma; right valve with grooved shelf along inside of most of antero- and posterodorsal margins to interlock with corresponding sharp, vertically elevated margins of left valve; posterior groove deeper, its anterior end thickened and elevated. Pallial line, pallial sinus and adductor muscle scars well defined, adult pallial sinus depth 41%–43% of shell length. Lithodesma stout (width 1.65 mm in shell 11.2 mm long), butterfly shaped, bilaterally asymmetrical, ligaments rather thick. Resilifers elevated; L-shaped on right valve, long oblique dorsoventral limb narrowly tapered, short anterodorsal limb at approximately right angle to it; anterolateral part of left valve resilifer smoothly curving to dorsoventral part, otherwise similar to right valve resilifer. Exterior sculptured with rounded commarginal ridges, weaker and fewer on left valve than on right. Periostracum set with minute, crowded, commarginally elongate, hexagonal, calcareous prisms that form outermost shell layer.

Distribution

Late Pleistocene (Castlecliffian) to Recent. Three Kings, North, South and Stewart Islands, 4–549 m; taken alive (rarely) at 12–549 m (Fig. 11B).

Remarks

Specimens from carbonate-rich substrata tend to attain larger size and have weaker commarginal ridges than specimens from mud, but otherwise appear indistinguishable in shell morphology. After repeated comparison of several hundred specimens, I have concluded that the two variants are ecophenotypes.

As indicated by the synonymy, *Hunkydora novozelandica* has been thoroughly confused with *Asthenothaerus maxwelli* n. sp., and *Thracia vitrea* (Hutton, 1873). Although similar in shape, *H. novozelandica* differs markedly from both these species in numerous details, principally: left valve far more weakly convex than right valve and seated well within perimeter of right valve in paired individuals, posterior of right valve strongly arched right, posterior of left valve flexed right to match right valve; prominent commarginal sculpture on right valve at an early stage of growth and on rostrum to maturity, both valves externally covered with a thin layer of minute, crowded, commarginally elongate, hexagonal prisms. Similarities in gross shell morphology between *Hunkydora* and *Thracia* species are probably due to convergence (see Harper *et al.* 2000).

Following Fleming (1951), *H. novozelandica* has consistently been interpreted as a subspecies of *H. australica* (Reeve, 1859), but the two are distinct species of *Hunkydora*, the eastern Australian one differing principally in being higher, in having the umbones situated further posteriorly and in that the anterior end of the inner posterodorsal margin of the right valve is thicker, higher and more tooth like. *Hunkydora australica* (three syntypes BMNH 1962695 examined), which is clearly referable to *Hunkydora*, was erroneously returned to *Thracia* by Lamprell and Healy (1998) without explanation.

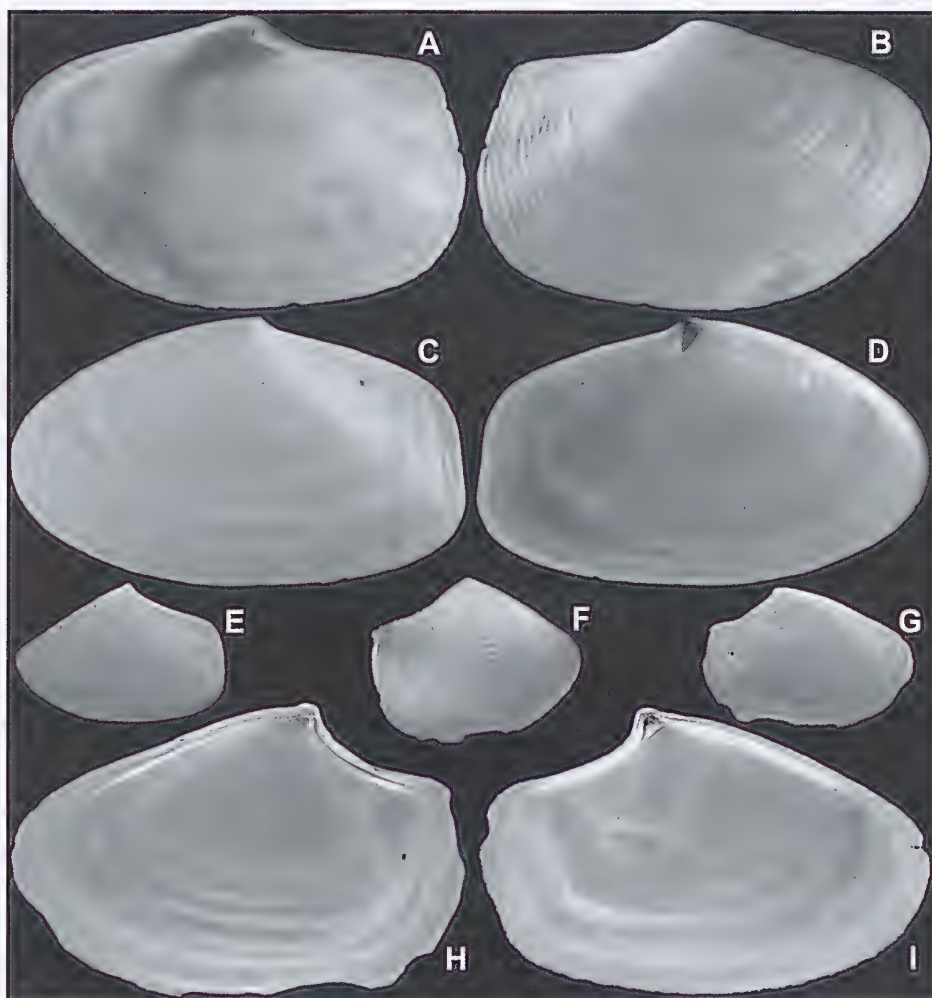


Fig. 9. Shells of *Hunkydora* species. A–F, *Hunkydora novozelandica* (Reeve, 1859): A,B, right valve, length 21.8 mm, W of Motuwheke Island, Bay of Islands, 42–43 m (M.96057); C,D, left valve, length 20.5 mm, Ranfurly Bank, East Cape, 103–106 m (M.71784); E,F, juvenile, length 4.85 mm, off Cape Brett, 80 m (M.35731). G–I, *Hunkydora rakiura* n. sp.: holotype, left (I) and right valve, length 5.20 mm, channel between Ulva Island and Bradshaw Peninsula, Paterson Inlet, Stewart Island, 33 m (M.152724).

Hunkydora rakiura n. sp.

Figs 4L, 9G–I, 11C

Hunkydora sp. Spencer *et al.* (in press).

Material examined

Holotype. Channel between Ulva Island and Bradshaw Peninsula, Paterson Inlet, Stewart Island, New Zealand, 46°56.5'S, 168°07.8'E, alive, 33 m, 12 Jan. 1952, MV *Alert* (pr, M.152724).

Paratypes. Off East Otago, Saunders Canyon, 45°56'S, 170°54'E, 360 m (3v, M.48858). Off Ruapuke Island, Foveaux Strait, oyster beds, 46°43'S, 168°30'E, 33–35 m (1v, M.71863).

Description

Shell up to 5.20 mm long, translucent white, inequilateral, right valve more inflated and higher than left, 1.4× longer than high; umbones opisthogyrous, at approximately posterior one-third; large, concave escutcheon bounded by angulation. Prodissoconch approximately 300 µm wide, almost circular, smooth; PI approximately 270 µm wide, globular. Dissoconch anterodorsal margin very broadly rounded or almost flat, posterodorsal margin concave, anterior margin tightly rounded, posterior margin obliquely subtruncate, ventral margin very broadly rounded. Antero- and posterodorsal margins of valves sharp, upright, margins of left valve seated against ventral side of margins of right valve on well-defined corresponding ledges. Right valve hinge with small tooth at anterior extremity of posterodorsal margin, otherwise edentulous, anterior and posterior parts of hinge area separated by triangular ligamental space; large resilifers sharply delineated, slightly elevated. Lithodesma unknown. Interior nacreous white, pallial sinus depth 40% of shell length. Adductor and anterior pedal retractor muscle scars well defined. Periostracum set with minute, crowded, commarginally elongate, hexagonal calcareous prisms that form outermost shell layer.

Distribution

South-eastern South Island and Stewart Island, 33–360 m; taken alive at 33 m from bryozoan/shell substratum (Fig. 11C)

Remarks

Hunkydora rakiura differs markedly from *H. novozelandica* in attaining considerably smaller size (length up to 5.20 v. 42 mm) and in having a larger prodissoconch (width 270–300 v. 220–250 µm). Comparing adults of *H. rakiura* with juveniles of *H. novozelandica* of the same shell size, *H. rakiura* differs further in being lower (length/height ratio right valve 1.40 v. 1.26) and in that the beaks are smaller, sharper and more strongly posterior, the anterior end is more broadly rounded, the posterodorsal margin is more deeply concave and the rostrum is dorsoventrally shorter and more weakly arched.

Etymology

After *rakiura*, the Maori name for Stewart Island, the type locality.

Superfamily CUSPIDARIOIDEA Dall, 1886

Family CUSPIDARIIDAE Dall, 1886

Genus *Pseudogrippina* n. gen.

Type species: *Pseudogrippina wanganellica* n. sp.; Recent, Wanganella Bank, southern Norfolk Ridge.

Diagnosis

Shell up to 2.80 mm long, roundly trigonal, posteriorly obliquely truncate, right valve with strong anterior tooth and no posterior tooth, left valve edentulous, resilifers sunken, lithodesma present, interior surface shell layer a chaotic mass of elongate prisms, thin periostracum minutely pitted.

Remarks

The type species of *Pseudogrippina* has striking similarity to *Grippina* species in shape and size, including the presence of a lithodesma set on sunken resilifers, but it differs in that the

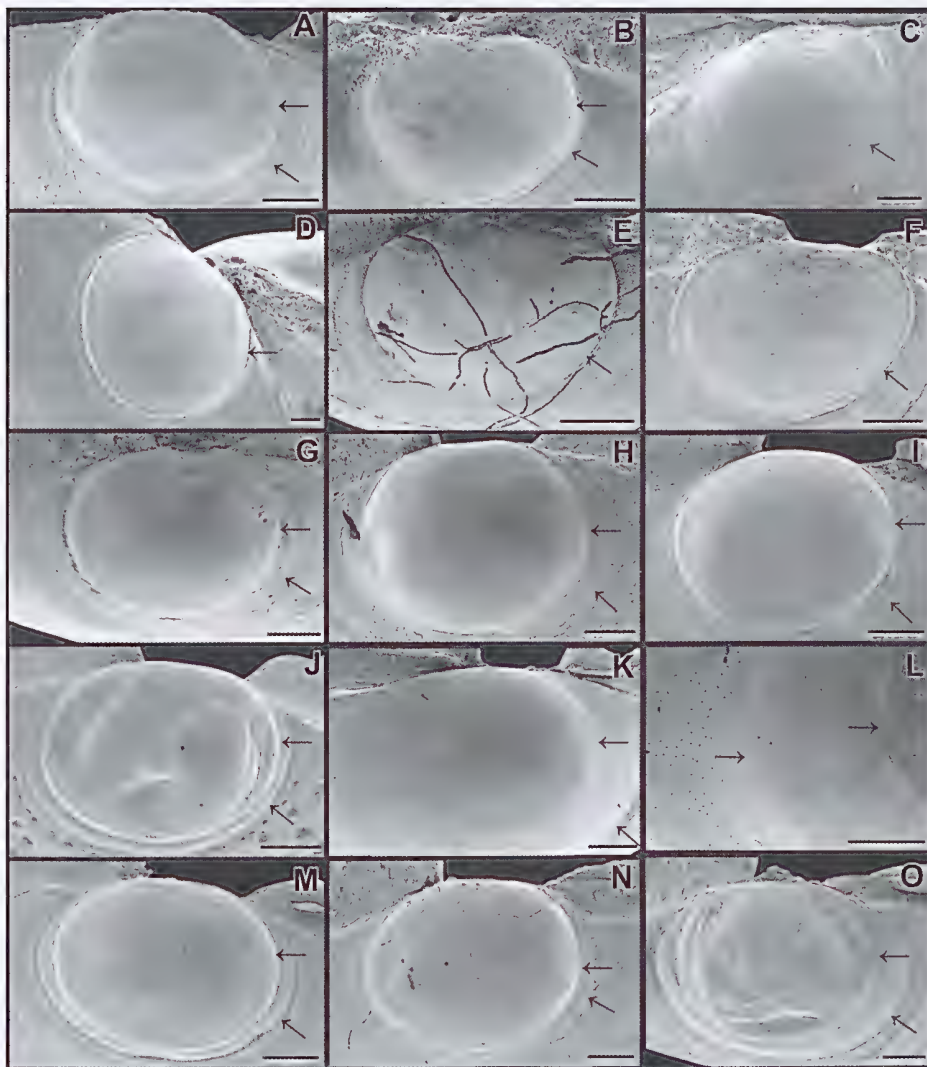


Fig. 10. Prodissococonchs of Cuspidariidae and Spheniopsidae (prodissococonch I and II boundaries or prodissococonch boundary indicated by arrows). *A*, *Plectodon regalis* n. sp., holotype, off Three Kings Islands, New Zealand, 91 m (M.152684). *B*, *Rhinoclama* (*Austronearea*) *brevirostris* Powell, 1937, SE of Great Island, 173–178 m (M.144426). *C*, *Rhinoclama* (*Austronearea*) *finlayi* Powell, 1937, N of Poor Knights Islands, 146 m (M.144424). *D*, *Rhinoclama* (*Austronearea*) *brooki* n. sp., holotype, SE of Nugent Island, Raoul Island, Kermadec Islands, 165–146 m (M.152685). *E*, *Rhinoclama* (*Austronearea*) *raoulensis* Powell, 1958, between Dayrell and Chanter Islets, Raoul Island, Kermadec Islands, 31–45 m (M.226999). *F*, *Rhinoclama* (*Austronearea*) *tangaroa* n. sp., paratype, Wanganella Bank, Norfolk Ridge, 437–422 m (M.234116). *G*, *Rhinoclama* (s. str.) *aupouria* (Dell, 1950), SE of Great Island, 173–178 m (M.144427). *H*, *Grippina aupouria* (Powell, 1937), 11 km NW of Great Island, Three Kings Islands, 310 m (M.93848). *I*, *Grippina rex* n. sp., holotype, off Three Kings Islands, 91 m (M.33807). *J*, *Grippina punctata* n. sp., holotype, off Spirits Bay, 63 m (M.152679). *K*, *L*, *Grippina globosa* n. sp., paratype, Middlesex Bank, NW of Three Kings Islands, 246–291 m (M.149490). *M*, *Grippina spirata* n. sp., holotype, off Spirits Bay, 63 m (M.149519). *N*, *Grippina acherontis* n. sp., paratype, off Patea, 40 m (M.53594). *O*, *Grippina pumila* n. sp., paratype, off Puysegur Point, 183 m (M.143883). Scale bars: 50 μ m.

right valve has only one relatively larger anterior hinge tooth, which stands obliquely instead of at a right angle to the valve plane, the inner surface shell layer is a chaotic mass of elongate prisms instead of smooth and the periostracum is minutely pitted throughout.

The presence of an anterior tooth, lack of a posterior tooth on the right valve and lack of teeth on the left valve are diagnostic characteristics of *Luzonia* Dall & E. A. Smith in Dall, 1890 (type species *Neaera philippinensis* Hinds, 1843; Recent, Philippine Islands; ICZN (1986)). Checking of the type material of *N. philippinensis* (BMNH 1961122) reveals that it comprises three specimens rather than a 'type specimen' as stated by Allen and Morgan (1981). Moreover, two species are represented, one by a complete right valve (length 5.65 mm), the other (smaller) by a live-taken closed pair and a complete right valve and a left valve hinge fragment, evidently from a single individual. Both show the hinge morphology diagnostic of *Luzonia* and both are posteriorly rostrate with small resilifers set in the hinge line. *Pseudoneaera wangellica* differs from these syntypes of *L. philippinensis* in numerous details, including a much shorter, obliquely truncate posterior end and correspondingly shallower pallial sinus, much stronger tooth on the right valve and in that the resilifers are sunken rather than within the hinge line. Placement of *Pseudogrippina* in Cuspidariidae is provisional pending knowledge of the anatomy.

The specimen selected as lectotype for *N. philippinensis* should, ideally, be the paired individual, but this formality is left to some future worker because I am reluctant to try and separate the valves.

Etymology

From the Greek *pseudos* (lie) + genus name *Grippina*.

Pseudogrippina wangellica n. sp.

Figs 3H,I, 4M, 11D, 12A,C, 21I

Material examined

Holotype. Wanganella Bank, Norfolk Ridge, summit, 32°34.4'S, 167°31.0'E, alive, 113 m, 29 Jan. 1981, RV *Tangaroa* (pr, M.152681).

Paratypes. Wanganella Bank: summit, 32°31.8'S, 167°29.5'E, 113–118 m (1v, M.257207); Norfolk Ridge, summit, 32°34.4'S, 167°31.0'E, alive, 113 m, (2pr, M.149523); E slope, 32°35.3'S, 167°41.8'E, 437–422 m (4v, M.234118); summit, 32°40.0'S, 167°33.6'E, 133 m (1pr, 4v, M.272623); summit, 32°39.2'S, 167°31.7'E, 133 m (6v, M.272622).

Description

Shell up to 2.80 mm long, ovate trigonal, of moderate thickness, moderately inflated, approximately 1.27× longer than high; beaks almost central, anterior end elongating slightly more rapidly than posterior in large specimens so that posterior end occupies 50%–54% of shell length; fresh specimens translucent white. Prodissoconch approximately 240 µm wide, prominent, oval, smooth; finely wrinkled, elevated, convex central area with shallow depression at summit, otherwise smooth; no PII discernable. Dissoconch anterior margin well rounded, smoothly merging with straight anterodorsal margin and broadly rounded ventral margin, posterodorsal margin very broadly rounded; posterior truncation short, broadly rounded or almost straight, oblique, extremities roundly angulate. Right valve with one strong, well-defined anterior hinge tooth, no posterior tooth, inner anterodorsal margin shelved to seat corresponding elevated narrow dorsal margin of left valve. Left valve edentulous. Lithodesma stout (width 230 µm in adult), longer than wide,

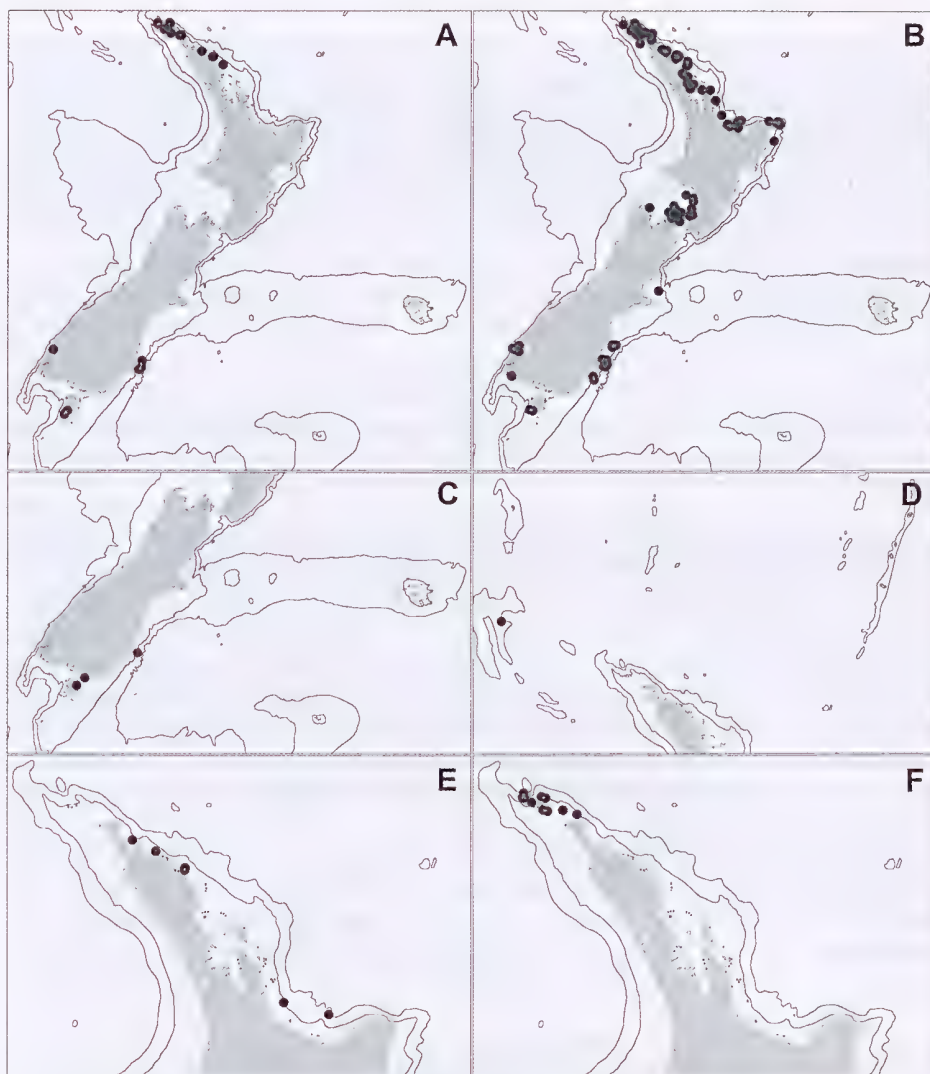


Fig. 11. Maps of the New Zealand region showing distributions of *Myochama*, *Hunkydora*, *Pseudogrippina* and *Plectodon* species (200 and 1000 m isobaths indicated). A, *Myochama tasmanica* (Tenison Woods 1877). B, *Hunkydora novozelandica* (Reeve, 1859). C, *Hunkydora rakiura* n. sp. D, *Pseudogrippina wangellica* n. sp. E, *Plectodon lepidus* n. sp. F, *Plectodon pruinus* n. sp.

subtriangular, rounded anteriorly, concave posteriorly, ligaments thin, sunken resilifers shallowly concave, slightly but distinctly elevated. Interior surface a layer of chaotically oriented, narrowly elongate prisms, pallial line and large adductor scars well defined; pallial sinus concave, depth approximately 30% of shell length. Exterior convex, posterior end flattened; sculptured throughout with weak, rounded commarginal ridges and faint radial lines. Periostracum thin, colourless, minutely pitted.

Distribution

Wanganella Bank, southern Norfolk Ridge, 133–437 m; taken alive at 113–133 m from substratum of rhodolith gravel and white biogenic sand (Fig. 11D).

Remarks

Pseudogrippina wanganellica resembles *Luzonia philippensis* (Hinds, 1843) (Philippines, depth unknown) and *L. simplex* (Allen & Morgan, 1981) (western Africa, 619–2357 m), but differs in shape (more ovate than trigonal, with shorter and higher rostrum), stronger commarginal sculpture, smaller size (length 2.8 v. 3.4 mm) and in that the resilifers are sunken rather than set in the hinge line. For additional remarks, see under *Pseudogrippina*.

Etymology

After Wanganella Bank, the type locality.

Genus *Plectodon* Carpenter, 1864

Plectodon Carpenter, 1864: 611. Type species (by monotypy): *Plectodon scaber* Carpenter, 1864; Recent, California.

Remarks

The four new species attributed to *Plectodon* described below resemble the holotype of *Plectodon scaber* (Palmer 1958: pl. 6, figs 6–8, subsequently fragmented) and other Californian specimens examined in gross shell morphology, including the presence of crisp calcareous granules set in the periostracum, and in having a substantial lithodesma set on oblique sunken resilifers (Coan *et al.* 2000: 559, pl. 121). However, they differ principally in attaining much smaller size (length up to 6.25 v. 19 mm), in that the sunken resilifers are simply shallow pits rather than distinctly elevated, the hinge teeth are smooth instead of pustulated dorsally and in being more weakly rostrate. *Plectodon scaber* differs further in that the posterior extremity of the anterodorsal margin of the right valve is spirally twisted immediately below the umbo.

The only other strictly similar species known to me is *P. granulatus* (Dall, 1881) from the western central Atlantic. Poutiers and Bernard (1995) referred *Neaera brazieri* E. A. Smith, 1885 (Australia) and *Cuspidaria ligula* Yokoyama, 1922 (Japan) to *Plectodon*, but, according to original descriptions, they lack granulate microsculpture.

Plectodon lepidus n. sp.

Figs 3J,K, 4N, 11E, 12B,D, 21J

Plectodon sp. 2 Spencer *et al.* (in press).

Material examined

Holotype. Off E side of Mayor Island, New Zealand, 37°18.9'S, 176°16.2'E, alive, 59–74 m, 22 Jan. 1979, RV *Tangaroa* (pr. M.152682).

Paratypes. Off Rangaunu Bay, 34°42.8'S, 173°14.5'E, 63 m (8v, M.149594). NW of Whangaroa Harbour, 34°54.0'S, 173°42.6'E, 83 m (1v, M.149596). Bay of Islands: off Twin Rocks, 35°10'S, 174°18'E, 46–73 m (3v, M.42188); 35°11.2'S, 174°16.7'E, 58–64 m (1v, M.96122); off island at entrance to Deep Water Cove, 35°11.9'S, 174°17.1'E, 47–49 m (1v, M.95725); off Deep Water Cove, fish gut (1v, M.112094). Whangaruru Harbour, dredged (2v, M.111956). Off E side of Mayor Island, 37°18.9'S, 176°16.2'E, alive, 59–74 m, (3 pr 17v, M.65656). Off White Island, 37°30.5'S, 177°09.7'E, 64–69 m, two stations (2v, M.149595; 2v, M.96298); 37°30.6'S, 177°09.7'E, 73–59 m (7v, M.94488).

Description

Shell up to 6.10 mm long, ovate-trigonal, of moderate thickness, moderately inflated, 1.52–1.60× longer than high; beaks almost central, fresh specimens translucent white with

narrow, opaque white radial rays. Prodissoconch approximately 230 µm wide, prominent, smooth; PI approximately 200 µm wide, globular. Dissoconch anterior margin well rounded, smoothly merging with straight anterodorsal margin and broadly rounded ventral margin; posterodorsal margin longer than anterodorsal, straight; posterior truncation more or less flat, slightly oblique, corners roundly angulate. Right valve with two strong, well-defined anterior and posterior hinge teeth, length of inner dorsal margins each with concave shelf to seat corresponding elevated narrow dorsal margins of left valve. Left valve with prominent, posteriorly inclined boss at posterior end of anterodorsal margin. Lithodesma stout (width 500 µm in adult), subtriangular, rounded anteriorly, concave posteriorly; ligaments thin, sunken resilifers shallowly concave. Interior with faint, shallow radial grooves that approximately coincide with white lines, pallial line and large adductor scars well defined; pallial sinus shallow, concave. Exterior convex, posterior area flattened, separated by low, broadly rounded angulation; crisply sculptured throughout with crowded, roughly hemispherical, calcareous granules set in thin periostracum, stronger on posterior area.

Distribution

North-eastern North Island (34°42.8'–37°30.6'S), 46–83 m; taken alive at 59–74 m from substratum of clean shell and stones (Fig. 11E).

Remarks

Two similar species occur in the New Zealand region and are described below. Another species occurs off Norfolk Island (1 left v, M.225171).

Etymology

From the Latin *elegans* (elegant).

Plectodon pruinosis n. sp.

Figs 3L, 4O, 11F, 12E–G

Plectodon sp. 3 Spencer *et al.* (in press).

Material examined

Holotype. Middlesex Bank, NW of Three Kings Islands, New Zealand, 33°57.0'S, 171°45.4'E, 98–103 m, 31 Jan. 1981, RV *Tangaroa* (right v, M.152683).

Paratypes. Off Three Kings Islands: Middlesex Bank, 33°57.0'S, 171°45.4'E, 98–103 m (2v, M.149573); Middlesex Bank, 33°59.9'S, 171°45.3'E, 186–196 m (3v, M.112807); Middlesex Bank, 34°00.9'S, 171°44.7'E, 201–216 m (2v, M.93232); 34°01'S, 172°07'E, 622 m (2v, M.34952); 13 km N of Great Island, 34°01.8'S, 172°12.0'E, 508 m (1v, M.149574); Middlesex Bank, 34°02.0'S, 171°44.0'E, 246–291 m (3v, M.149571); Middlesex Bank, 34°02.1'S, 171°45.8'E, 221–206 m (1v, M.149570); 24 km NW of Great Island, 34°05.9'S, 171°55.1'E, 710 m (2v, M.94367); S of Great Island, 34°14.1'S, 172°09.0'E, 192–202 m (1v, M.149575); 34°14.8'S, 172°13.6'E, SE of Great Island, 173–178 m (1v, M.149572). NW of Cape Reinga, 34°14.2'S, 172°32.4'E, 100 m (3v, M.149576). Off Spirits Bay, 34°18.36'S, 172°49.39'E, 68 m (1v, M.152487).

Description

Shell up to 6.25 mm long, ovate-trigonal, of moderate thickness, moderately inflated, 1.60–1.79× longer than high; beaks almost central, fresh specimens translucent white. Prodissoconch approximately 230 µm wide, prominent, convex, central area elevated, finely wrinkled dorsally, minutely and densely maleate; no PII. Dissoconch anterior margin well rounded, smoothly merging with broadly rounded anterodorsal and ventral margins;

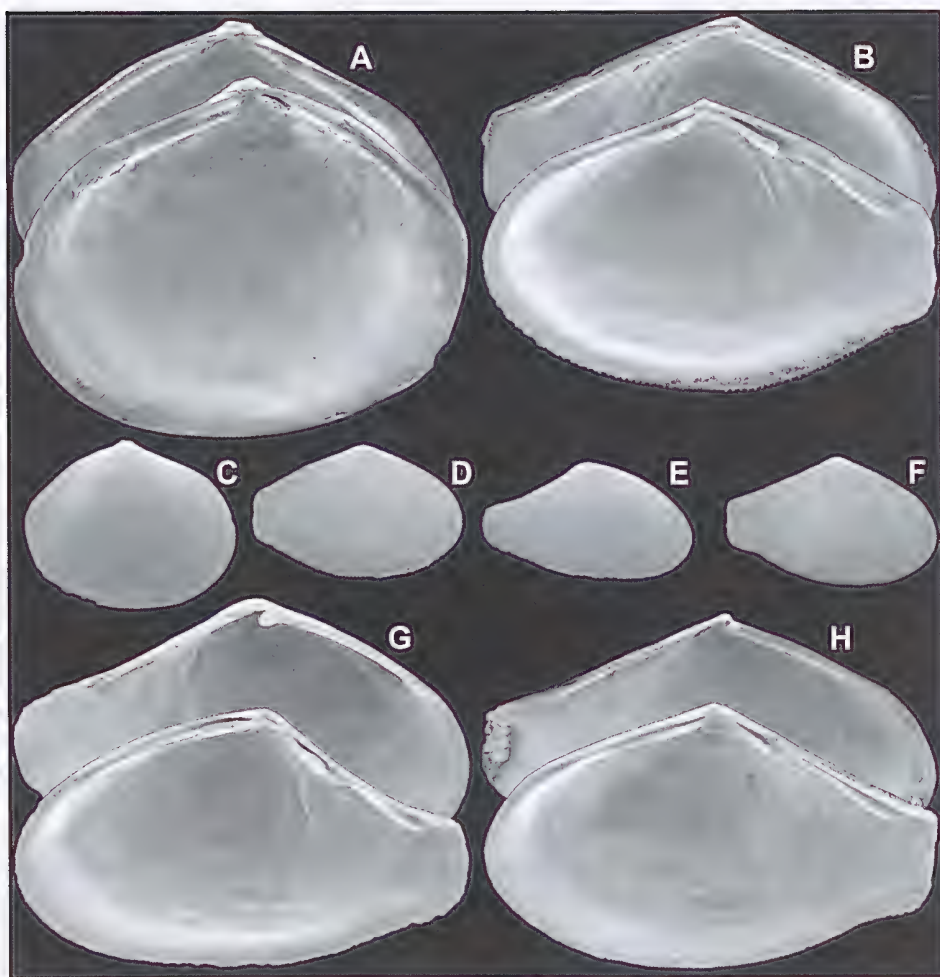


Fig. 12. Shells of *Pseudogrippina* and *Plectodon* species. *A,C*, *Pseudogrippina wangellica* n. sp.: holotype, left (*A* upper) and right valve, length 2.30 mm, Wanganella Bank summit, Norfolk Ridge, 113 m (M.152681). *B,D*, *Plectodon lepidus* n. sp.: holotype, left (*B* upper) and right valve, length 5.25 mm, off E side of Mayor Island, 59–74 m (M.152682). *E,G*, *Plectodon pruinosis* n. sp.: holotype, right valve (*E,G* lower), length 5.72 mm (M.152683), and paratype, left valve (*G* lower), length 4.63 mm (M.149573), Middlesex Bank, NW of Three Kings Islands, 98–103 m. *F,H*, *Plectodon regalis* n. sp.: holotype, left (*H* upper) and right valve, length 5.20 mm, off Three Kings Islands, 91 m (M.152684).

posterodorsal margin straight; posterior truncation broadly rounded or flat, slightly oblique, corners tightly rounded. Right valve with two strong, well-defined anterior and posterior hinge teeth, length of inner dorsal margins each with concave shelf to seat corresponding elevated narrow dorsal margins of left valve. Left valve with prominent, posteriorly inclined boss at posterior end of anterodorsal margin. Resilifers sunken, oblique, elongate-oval, concave, ventral margin slightly elevated (lithodesma almost certainly present although missing in isolated valves). Interior with faint, shallow radial grooves, pallial line and large adductor scars well defined, pallial sinus broad and shallow. Exterior convex, posterior area weakly convex, separated by low, broadly rounded angulation; crisply sculptured

throughout with crowded, roughly hemispherical, calcareous granules set in thin periostracum, stronger on posterior area.

Distribution

Off Three Kings Islands and off Spirits Bay, 98–710 m (shells only), from comminuted bryozoan/shell substrata (Fig. 11F).

Remarks

Plectodon pruinus differs from *P. lepidus* in having shallowly curved rather than flat dorsal margins, finer granulate sculpture, a larger prodissoconch with a more elevated central area, a dorsoventrally shorter posterior truncation and in that the pallial sinus is broader. The two species are allopatric. *Plectodon pruinus* occurs sympatrically with the species described below.

Etymology

From the Latin *pruinus* (frosty).

Plectodon regalis n. sp.

Figs 3M, 10A, 12F,H, 15A, 21K

Cuspidaria aupouria. – Crozier, 1966: 46, figs 16, 17; Powell, 1979: 436. In part + three undescribed species of *Cuspidaria*. Not Dell, 1950.

Plectodon sp. 1 Spencer *et al.* (in press).

Material examined

Holotype. Off Three Kings Islands, New Zealand, 34°11'S, 172°10'E, alive, 91 m, 19 Feb. 1974, RV *Acheron* (pr, M.152684).

Paratypes. Off Three Kings Islands: Middlesex Bank, 33°57.0'S, 171°45.4'E, 98–103 m (2v, M.149582); King Bank, 33°57.4'S, 172°19.4'E, alive, 128–123 m (1pr, 1v, M.149581); Middlesex Bank, 33°59.8'S, 171°46.8'E, 143–163 m (1v, M.149597); Middlesex Bank, 34°01.2'S, 171°44.4'E, 206–211 m (1v, M.149579); 13 km N of Great Island, 34°01.8'S, 172°12.0'E, 508 m (3v, M.149583); 37 km NW of Great Island, 34°02.0'S, 171°48.4'E, 188 m (3v, M.64914); Middlesex Bank, 34°02.0'S, 171°44.0'E, 246–291 m (3v, M.149586); 11 km NW of Great Island, 34°06.5'S, 172°04.7'E, 310 m (1v, M.149577); off North-east Island, 34°08.5'S, 172°11'E, 102 m (1v, M.34534); 34°11'S, 172°10'E, alive, 91 m (1v, M.33801); S of Great Island, alive, 34°14.1'S, 172°09.0'E, 192–202 m (2pr, 3v, M.149580); 34°20.2'S, 172°21.8'E, 121 m (1v, M.149578); 28 km S of Great Island, 34°24.0'S, 172°16.8'E, 120 m (2v, M.149584). NW of Cape Reinga, 34°14.2'S, 172°32.4'E, 100 m (1v, M.94571); 34°22.8'S, 172°24.6'E, alive, 121 m (5pr, 4v, M.149585). N of Cape Reinga, 34°21'S, 172°37'E, alive, 88 m (1pr, 2v, M.36002).

Other material examined. Three Kings Trough, NW of Three Kings Islands, 34°00'S, 171°55'E, 805 m (1v, M.149809).

Description

Shell up to 6.10 mm long, ovate-trigonal, of moderate thickness, moderately inflated, approximately 1.7× longer than high; anterior end slightly longer than posterior, fresh specimens translucent white with irregular, opaque white radial rays. Prodissococonch approximately 220 µm wide, prominent, convex, smooth; PI approximately 200 µm wide, globular. Dissococonch anterior margin well rounded, smoothly merging with straight anterodorsal and broadly rounded ventral margin; posterodorsal margin straight; posterior truncation more or less flat, slightly oblique, corners tightly rounded. Right valve with two strong, well-defined anterior and posterior hinge teeth, length of inner dorsal margins each with concave shelf to seat corresponding elevated narrow dorsal margins of left valve. Left

valve with prominent, posteriorly inclined boss at posterior end of anterodorsal margin. Lithodesma stout (width 570 μm in adult), about as long as broad, rounded anteriorly, concave posteriorly; ligaments thin, sunken resilifers shallowly concave. Interior with faint radial lines, pallial line and large adductor scars well defined; pallial sinus broad and shallow, angulate dorsally. Exterior convex, posterior area weakly convex, separated by low, broadly rounded angulation; crisply sculptured throughout with crowded, columnar, calcareous granules set in thin periostracum, stronger on posterior area.

Distribution

Off Three Kings Islands, 88–805 m; taken alive at 88–202 m from comminuted bryozoan/shell substrata (Fig. 15A).

Remarks

Plectodon regalis differs from the allopatric species *P. lepidus* in having considerably finer granulate sculpture, in being slightly more elongate and in that the posterior truncation is slightly shorter dorsoventrally. It differs from the sympatric species *P. pruinus* in being less inflated and having flat, instead of broadly curved, dorsal margins, taller sculptural granules and a weaker swelling on the central area of the prodissoconch.

Etymology

From the Latin *regalis* (royal).

Plectodon sp.

Material examined

N of Norfolk Island, 28°59'S, 167°58'E, 38 m (1v, M.225171).

Distribution

Off Norfolk Island, 38 m (1v only).

Remarks

A single left valve (length 3.95 mm) from off Norfolk Island has flat dorsal margins, as in *P. lepidus* and *P. regalis*, but has finer sculpture than *P. lepidus*, coarser sculpture than *P. regalis* and is more inequilateral than both. It clearly represents a distinct, undescribed species, although I am reluctant to base a new taxon on a single valve, particularly a left one.

Genus *Rhinoclama* Dall & E. A. Smith in Dall, 1886

Rhinoclama Dall & Smith in Dall, 1886: 300. Type species (ICZN Opinion 1376 (1986)): *Cuspidaria* (*Rhinoclama*) *adamsi* Morgan & Heppell in Allen & Morgan, 1981; Recent, Philippines.

Rhinoclama (s. str.) *aupouria* (Dell, 1950) n. comb.

Figs 10G, 14B,C, 15B, 16B,D, 21N

Cuspidaria aupouria Dell, 1950: 21, figs 3, 4; Powell, 1979: 436 (in part = three undescribed species of *Cuspidaria* + *Plectodon regalis*).

Cuspidaria (*Rhinoclama*) *aupouria*. – Poutiers & Bernard, 1995: 156.

NOT *Cuspidaria aupouria*. – Crozier, 1966: 46, figs 16, 17 (= three undescribed species of *Cuspidaria* + *Plectodon regalis*).

Material examined

Holotype. N of North Cape, New Zealand, 34°18'S, 173°02'E, 137 m, J. A. Bollons, SS *Hinemoa* (rv, M.4726).

Other material examined. Off Three Kings Islands: 34°00'S, 171°55'E, 805 m (3v, M.144430); submarine cave, S side Rosemary Rock, 34°10.8'S, 172°03.00'E, 20 m (1v, M.117166); 11 km NW of Great Island, 34°06.5'S, 172°04.7'E, 310 m (1v, M.149587); off West Island, *Elingamite* wreck, 34°11'S, 172°03'E, 37 m (1v, M.154154); 34°14.8'S, 172°13.6'E, alive, 173–178 m (7pr, 4v, M.144427); 39 km SW of Great Island, 34°17.6S, 171°45.3'E, 427 m (4v, M.94252); 28 km S of Great Island, 34°24.0'S, 172°16.8'E, 120 m (2v, M.144428). Off Mayor Island, 37°16.7'S, 176°17.5'E, 104–109 m (1v, M.144429). Ranfurly Bank, East Cape: 37°32.8'S, 178°48.7'E, alive, 94 m (3pr, 24v, M.144433); 37°33.1'S, 178°49.5'E, 94–89 m (3v, M.144431); 37°33.2'S, 178°50.3'E, 76–71 m (2v, M.71542); 37°33.4'S, 178°48.3'E, alive, 106–103 m (2pr, 7v, M.71792); 37°37.8'S, 178°52.4'E, 50–72 m (1v, M.96179); 37°38.4'S, 178°51.7'E, 79–83 m (5pr, 3v, M.96349).

Description

Shell up to 5.40 mm long, ovate-trigonal, stout, inflated, approximately 1.4× longer than high, anterior end 37%–42% of shell length, antero- and posterodorsal margins of right valve overlapping those of left; translucent white with narrow, opaque white radial rays; periostracum thin, buff. Prodissoconch approximately 230 µm wide, subcircular, very finely maleate, wrinkled, PI approximately 200 µm wide, globular. Dissoconch anterior margin well rounded, smoothly merging with flat or very weakly convex anterodorsal margin and broadly convex ventral margin; posterodorsal margin more or less straight; posterior truncation weakly convex, oblique, corners tightly rounded. Right valve with two strong, well-defined anterior and posterior hinge teeth, posterior tooth considerably larger, length of inner dorsal margins shelved, strongly so posteriorly, to seat corresponding elevated narrow dorsal margins of left valve. Left valve edentulous. Resilifers sunken, narrowly ovate concave, lithodesma trigonal. Pallial line and large adductor scars well defined; pallial sinus broad, concave. Exterior convex, posterior area strongly flattened and bounded by tightly rounded angulation; posterodorsal margin of both valves margined by sharp angulation; anterodorsal margin bounded by rounded angulation. Early dissoconch covered with minute punctae; thereafter flattened rostral area with coarse, crowded granules, elsewhere matt.

Distribution

Off Three Kings Islands, Mayor Island and Ranfurly Bank, East Cape, 20–805 m; taken alive at 71–178 m from comminuted bryozoan/shell substrata (Fig. 15B).

Remarks

Cuspidaria aupouria Dell, 1950, resembles the type species of *Austroneaera* and congeners from the New Zealand region in gross shell morphology, but differs significantly by having much stronger, more crowded granules on the rostral area, a distinct rostral angulation, microscopic punctae on the early dissoconch, a distinctly thicker shell, angulations bounding both the antero- and posterodorsal margins, a pattern of opaque white rays and a stronger area on the right valve. Shell thickness and rostral sculpture approach the conditions in New Zealand *Plectodon* species, all of which have, however, strong exterior sculpture throughout and a prominent boss at the posterior end of the anterodorsal margin. Because *C. aupouria* clearly does not belong in *Rhinoclama* (*Austroneaera*), it is tentatively referred to *Rhinoclama* (*s. str.*), although the rostrum is shorter and the commarginal sculpture considerably weaker than in the type species.

The six valves identified as *Cuspidaria aupouria* by Crozier (1966; off Three Kings Islands, 805 m) prove to comprise a mixture of three undescribed species of *Cuspidaria* (M.20826, 149807, 149808) and a specimen of *Plectodon regalis* n. sp. (M.149809).

Subgenus *Austroneaera* Powell, 1937

Austroneaera Powell, 1937a: 174. Type species (by original designation): *Austroneaera brevirostris* Powell, 1937; Recent, New Zealand.

Remarks

Allen and Morgan (1981) interpreted *Austroneaera* as a synonym of *Rhinoclama* because of similarity between their type species in gross shell morphology. They are also similar in the presence of a lithodesma set on sunken resilifers, although Morgan and Heppell (in Allen and Morgan 1981) failed to mention these characteristics in their description of the holotype of *R. adamsi*. However, the type species of *Austroneaera* differs in that the posterior area is defined by a low, rounded angulation rather than an elevated, well-defined ridge and in lacking prominent commarginal ridges (misleadingly described as 'striations' by Morgan and Heppell (in Allen and Morgan 1981) in their description of *R. adamsi*). Regrettably, the holotype of *R. adamsi* has been severely damaged by Byrne's disease, so it is impossible to tell whether it has the minute, thinly distributed, calcareous periostracal granules characteristic of the type species of *Austroneaera* and most other congeners from the New Zealand region. Whatever the case, relatively coarse, crowded granules, such as those characteristic of *Plectodon* species, are certainly absent.

Poutiers and Bernard (1995) interpreted *Austroneaera* as a synonym of *Rhinoclama*, which they grouped as a subgenus of *Cuspidaria* Nardo, 1840, stating (p. 148) that the '... general arrangement of the genus depends on the type and presence of hinge teeth, which seem rather mutable'. I prefer a more conservative approach and follow Krylova (1994), who interpreted *Austroneaera* as a subgenus of *Rhinoclama*.

Rhinoclama (Austroneaera) brevirostris Powell, 1937

Figs 3N, 10B, 13A,C, 15C, 21L

Austroneaera brevirostris Powell, 1937a: 174, pl. 48, fig. 11; Powell, 1979: 438, pl. 79, fig. 18.

Cuspidaria (Rhinoclama) brevirostris. – Poutiers & Bernard, 1995: 157.

Material examined

Holotype. 34°13.3'S, 172°12.0'E, off Three Kings Islands, New Zealand, 260 m, 17 Aug. 1932, RRS *Discovery II* (1v, BMNH 1962950).

Other material examined. Off Three Kings Islands: Three Kings Trough, 34°00'S, 171°55'E, 805 m (1v, M.17522); Middlesex Bank, 34°00.9'S, 171°44.7'E, alive, 201–216 m (1pr, 10v, M.93234); Middlesex Bank, 34°01.2'S, 171°44.4'E, alive, 206–211 m (1pr, 4v, M.144420); Middlesex Bank, 34°02.0'S, 171°44.0'E, 246–291 m (11v, M.144421); 11 km NW of Great Island, 34°06.5'S, 172°04.7'E, alive, 310 m (5v, 1pr, M.93861); S of Great Island, 34°14.1'S, 172°09.0'E, 192–202 m (2v, M.149801); SE of Great Island, 34°14.8'S, 172°13.6'E, alive, 173–178 m (6pr, 16v, M.144426); 37 km SW of Great Island, 34°20.4'S, 171°48.2'E, 440 m (1v, M.144423). Ranfurly Bank, East Cape: 37°32.8'S, 178°48.7'E, alive, 94 m (5pr, 11v, M.60800); 37°33.1'S, 178°49.5'E, alive, 94–89 m (10pr, 20v, M.74703); 37°33.2'S, 178°50.3'E, alive, 76–71 m (1pr, 1v, M.70542); 37°33.4'S, 178°48.3'E, alive, 106–103 m (9pr, 64v, M.70791). Rungapapa Knoll, WNW of White Island, 37°33.8'S, 176°59.0'E, alive, 188–228 m (13pr, 9v, M.113550). Bradshaw Basin floor, Bradshaw Sound, 45°17.3'S, 167°02.6'E, 415 m (1pr, M.138711). Utah Basin floor, Doubtful Sound, 45°17.9'S, 166°55.5'E, 400 m (1v, M.144425).

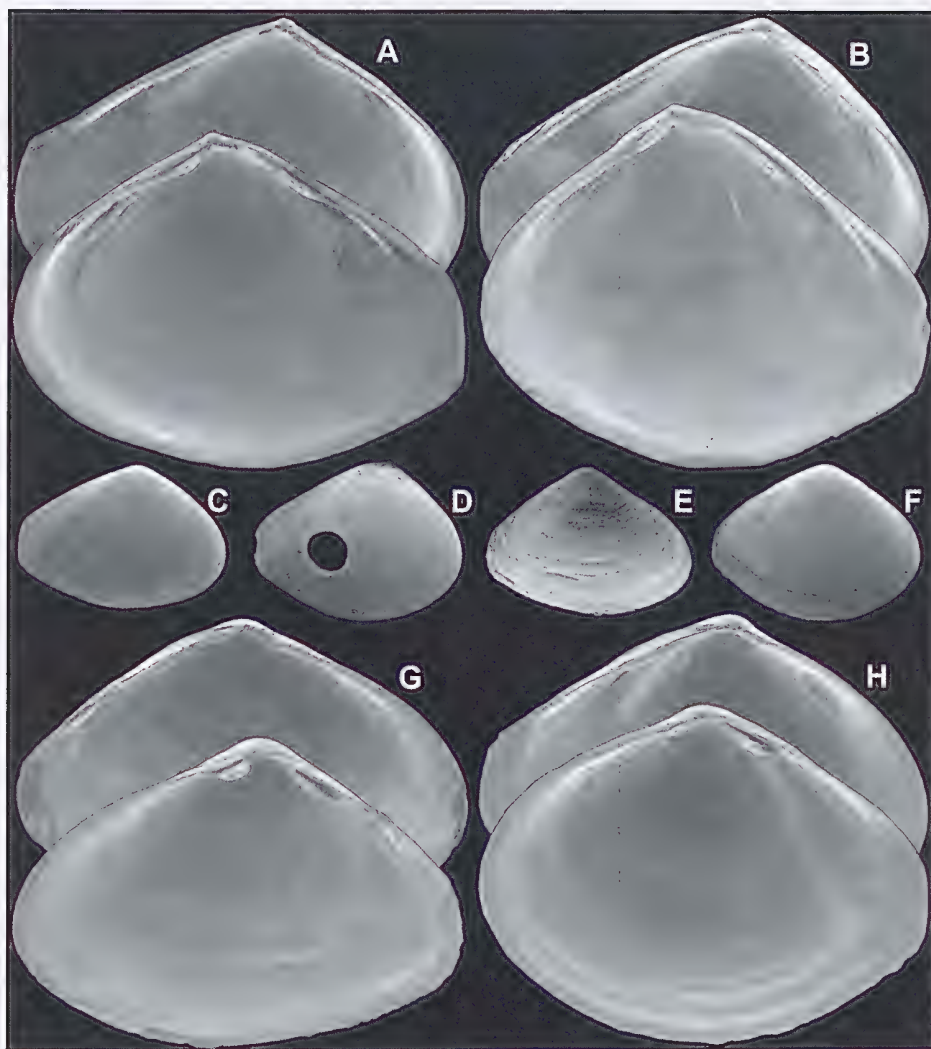


Fig. 13. Shells of *Rhinoclama* (*Austroneaera*) species. *A,C*, *Rhinoclama* (*Austroneaera*) *brevirostris* Powell, 1937: left (*A* upper) and right valves, length 3.70 mm, SE of Great Island, 173–178 m (M.144426). *B,D*, *Rhinoclama* (*Austroneaera*) *finlayi* Powell, 1937: left (*B* upper) and right valves, length 2.90 mm, N of Poor Knights Islands, 146 m (M.144424). *E,G*, *Rhinoclama* (*Austroneaera*) *raoulensis* Powell, 1958: left (*G* upper) and right valves, length 3.80 mm, between Dayrell and Chanter Islands, 31–45 m (M.226999). *F,H*, *Rhinoclama* (*Austroneaera*) *brooki* n. sp.: holotype, left (*H* upper) and right valve, length 5.00 mm, SE of Nugent Island, Raoul Island, Kermadec Islands, 165–146 m (M.152685).

Description

Shell up to 4.40 mm long, ovate-trigonal, thin, inflated, 1.33–1.43× longer than high, translucent white, beaks distinctly opisthogyrous, anterior end 47%–51% of shell length, antero- and posterodorsal margins of right valve overlapping those of left. Prodissoconch approximately 200 µm wide, subcircular, surface exceedingly finely maleate, PI approximately 180 µm wide, globular. Dissoconch anterior margin well rounded, smoothly

merging with flat or very weakly convex anterodorsal margin and broadly convex ventral margin; posterodorsal margin more or less straight; posterior truncation weakly convex, slightly oblique, corners tightly rounded. Right valve with two strong, well-defined anterior and posterior hinge teeth, posterior tooth considerably larger, length of inner dorsal margins weakly shelved to seat corresponding elevated narrow dorsal margins of left valve. Left valve edentulous. Lithodesma stout (width 400 μm in adult), about as long as wide, subtriangular, concave posteriorly; ligaments thin, narrowly ovate sunken resilifers concave. Interior with weak radial grooves, pallial line and large adductor scars well defined; pallial sinus broad, shallow, concave. Exterior convex, posterior area flattened and separated by broadly rounded angulation, posterodorsal margin of both valves bounded by sharp angulation; sculptured with fine commarginal growth lines and extremely small, thinly distributed calcareous granules set in thin, shiny, pale buff periostracum.

Distribution

Three Kings Islands, NE North Island, and Fiordland, 71–805 m; taken alive at 71–310 m from comminuted bryozoan/shell substrata (Fig. 15C).

Remarks

Three specimens from Fiordland resemble *R. (A.) brevirostris* rather than *R. (A.) finlayi* in shape. Assuming they are *R. (A.) brevirostris*, the lack of intermediate populations would suggest a relictual distribution.

Rhinoclama (Austroneaera) finlayi Powell, 1937

Figs 10C, 13B,D, 15D

Austroneaera finlayi Powell, 1937a: 175, pl. 48, fig. 12; Powell, 1979: 438, pl. 79, fig. 17.

Cuspidaria (Rhinoclama) finlayi. – Poutiers & Bernard, 1995: 159.

NOT *Austroneaera finlayi*. – Dell, 1956: 168 (= *Cuspidaria (Pseudoneaera) wellmani* (Fleming, 1948)).

Material examined

Holotype. Off Poor Knights Islands, New Zealand, 110 m (1v, AIM AK70071).

Other material examined. N of North Cape, 34°20.0'S, 173°06.6'E, 163–168 m (1v, M.144422). Off Poor Knights Islands: 35°22'S, 174°43'E, alive, 146 m (6pr, 20v, M.144424); 35°29'S, 174°43.5'E, 110 m (7v, M.67870). Off Mayor Island, 37°15.2'S, 176°14.5'E, 188–193 m (1v, M.60990); 37°16.7'S, 176°17.5'E, alive, 104–109 m (4pr, 12v, M.67497). Off White Island, 37°31'S, 177°08'E, 213 m (1pr, 2v, M.10363).

Description

Shell up to 3.50 mm long, ovate–trigonal, thin, inflated, 1.20–1.32 \times longer than high, translucent white, beaks distinctly opisthogyrous, anterior end 42%–43% of shell length, antero- and posterodorsal margins of right valve overlapping those of left. Prodissoconch approximately 200 μm wide, subcircular, smooth, PII not apparent. Dissoconch anterior margin well rounded, smoothly merging with flat or very weakly convex anterodorsal margin and broadly convex ventral margin; posterodorsal margin more or less straight; posterior truncation weakly convex, slightly oblique, corners tightly rounded. Right valve with two strong, well-defined anterior and posterior hinge teeth, posterior tooth considerably larger, length of inner dorsal margins weakly shelved to seat corresponding elevated narrow dorsal margins of left valve. Left valve edentulous. Lithodesma stout, narrowly ovate sunken resilifers concave. Interior with weak radial grooves, pallial line and large adductor scars well defined; pallial sinus broad, shallow, concave. Exterior convex,

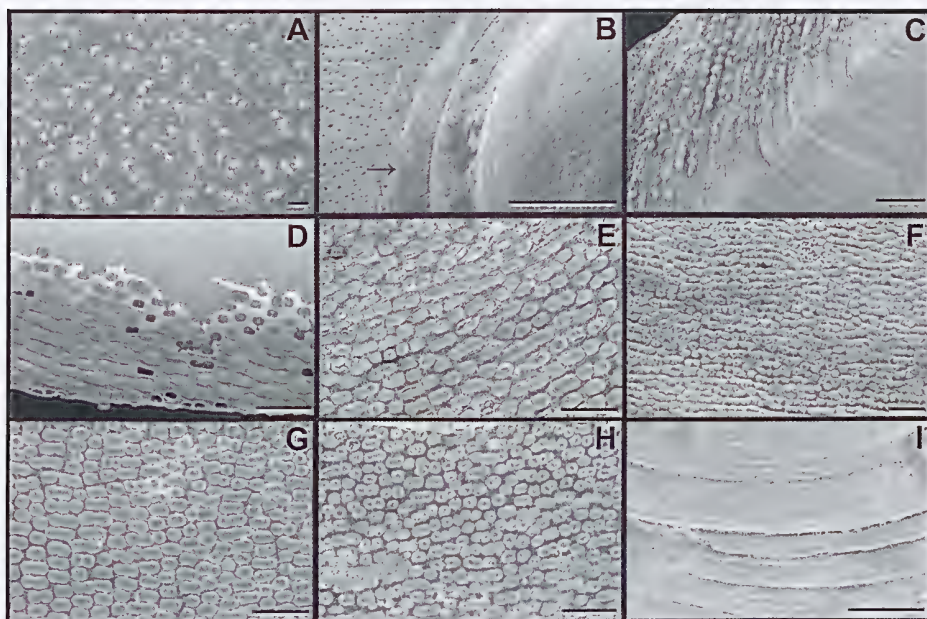


Fig. 14. Dissoconch microsculpture of Cuspidariidae and Spheniopsidae (exterior, right valve and adult unless indicated). *A*, *Rhinoclama (Austroneaera) brooki* n. sp., holotype, SE of Nugent Island, Raoul Island, Kermadec Islands, 165–146 m (M.152685). *B,C*, *Rhinoclama (s. str.) aupouria* (Dell, 1950), prodissoconch and early dissoconch (*B*, boundary arrowed) and adult posterodorsal area (*C*), SE of Great Island, Three Kings Islands, 173–178 m (M.144427). *D*, *Grippina aupouria* (Powell, 1937), view showing free edge of periostracum folded around ventral margin onto interior surface of adult right valve (demonstrating that calcareous beads are periostracal), Middlesex Bank, 201–216 m (M.93236). *E*, *Grippina rex* n. sp., holotype, off Three Kings Islands, 91 m (M.33807). *F*, *Grippina punctata* n. sp., holotype, off Spirits Bay, 63 m (M.152679). *G*, *Grippina spirata* n. sp., holotype, off Spirits Bay, 63 m (M.149519). *H*, *Grippina acherontis* n. sp., holotype, off Patea, 40 m (M.152680). *I*, *Grippina pumila* n. sp., holotype, off Puysegur Point, 183 m (M.152677). Scale bars: *B*, 25 μ m; others, 50 μ m.

posterior area flattened, posterodorsal margin of both valves bounded by sharp angulation; sculptured with fine commarginal growth lines and minute, thinly distributed calcareous granules set in thin, shiny, pale buff periostracum.

Distribution

Off North Cape and Poor Knights, Mayor and White Islands, North-eastern North Island, 110–213 m; taken alive at 104–146 m from muddy substrata (Fig. 15*D*).

Remarks

Compared with *R. (A.) brevirostris*, *R. (A.) finlayi* differs in being more narrowly trigonal (length/width ratio right valves 1.20–1.32, mean 1.259, SD 0.037, $n = 10$: as against 1.33–1.48, mean 1.418, SD 0.043, $n = 10$; and 1.32–1.43, mean 1.371, SD 0.040, $n = 10$ for *R. (A.) brevirostris* from off the Three Kings Islands and Ranfurly Bank, East Cape respectively), in attaining a smaller size (length up to 3.5 v. 4.40 mm), in that the shelf inside the posterodorsal margin of the right valve extends further posteriorly and in that the shell wall is distinctly thicker. Approximately 10% of specimens of *R. (A.) brevirostris* are as narrowly trigonal as *R. (A.) finlayi*, although all seen are larger than the few broadly trigonal

specimens of *R. (A.) finlayi*. Most specimens of *R. (A.) finlayi* are also more inflated than *R. (A.) brevirostris* and have flatter area on rostrum. *Rhinoclama (A.) finlayi* has its distributional range within that of *R. (A.) brevirostris* and lives in muddy substrata rather than clean bryozoan/shell hash. *Rhinoclama (A.) finlayi* may ultimately prove to be an ecophenotypic variant of *R. (A.) brevirostris*, although supportive comparative anatomical data are wanting.

Juveniles of *R. (A.) finlayi* and *R. (A.) brevirostris* are superficially similar to *Cuspidaria (Pseudoneaera) wellmani* (Fleming, 1948), but are immediately separable by the sunken resilifers (in hinge line in *P. wellmani*), the broader lithodesma and the stronger hinge teeth. Specimens of *C. wellmani* from off the Chatham Islands (M.10849–51) were misidentified as *R. (A.) finlayi* by Dell (1956), the latter species being unknown from the Chatham Islands.

Rhinoclama (Austroneaera) raoulensis Powell, 1958

Figs 3O, 10E, 13E–G, 15E, 21M

Austroneaera raoulensis Powell, 1958: 78, pl. 9, fig. 9.

Cuspidaria (Rhinoclama) raoulensis. – Poutiers & Bernard, 1995: 165.

Material examined

Holotype. 29°15'S, 177°51'W, off Raoul Island, Kermadec Islands, New Zealand, 75–85 m, RV *Galathea* (rv, Zoological Museum, Copenhagen).

Other material examined. Off Meyer Island, Raoul Island, Kermadec Islands, 29°14.7'S, 177°52.7'W, alive, 27–22 m (3pr, 1v, M.225814). Between Dayrell and Chanter Islets, Raoul Island, 29°15.00'S, 177°50.90'W, alive, 31–45 m (1pr, M.226999).

Description

Shell up to 3.80 mm beaks distinctly opisthogyrous, anterior end 45%–52% of shell length, antero- and posterodorsal margins of right valve overlapping those of left. Prodissoconch approximately 170 µm wide, subcircular, smooth, long, elongate-trigonal, thin, inflated, 1.54–1.64× longer than high, translucent white, PII not apparent. Dissoconch anterior margin well rounded, smoothly merging with flat or very weakly convex anterodorsal margin and broadly convex ventral margin; posterodorsal margin more or less straight; posterior truncation weakly convex, slightly oblique, corners tightly rounded. Right valve with two strong, well-defined anterior and posterior hinge teeth, posterior tooth considerably larger, length of inner dorsal margins weakly shelved to seat corresponding elevated narrow dorsal margins of left valve. Left valve edentulous. Lithodesma stout (width 300 µm in adult), ligaments thin, narrowly ovate sunken resilifers concave. Pallial line and large adductor scars well defined; pallial sinus broad, shallow. Exterior convex, posterior area flattened, posterodorsal margin of both valves bounded by low, rounded angulation; sculptured with fine commarginal growth lines and extremely small, thinly distributed calcareous granules set in thin, shiny, translucent, pale buff periostracum.

Distribution

Raoul Island, Kermadec Islands, 22–85 m; taken alive at 22–45 m from clean basaltic sand (Fig. 15E).

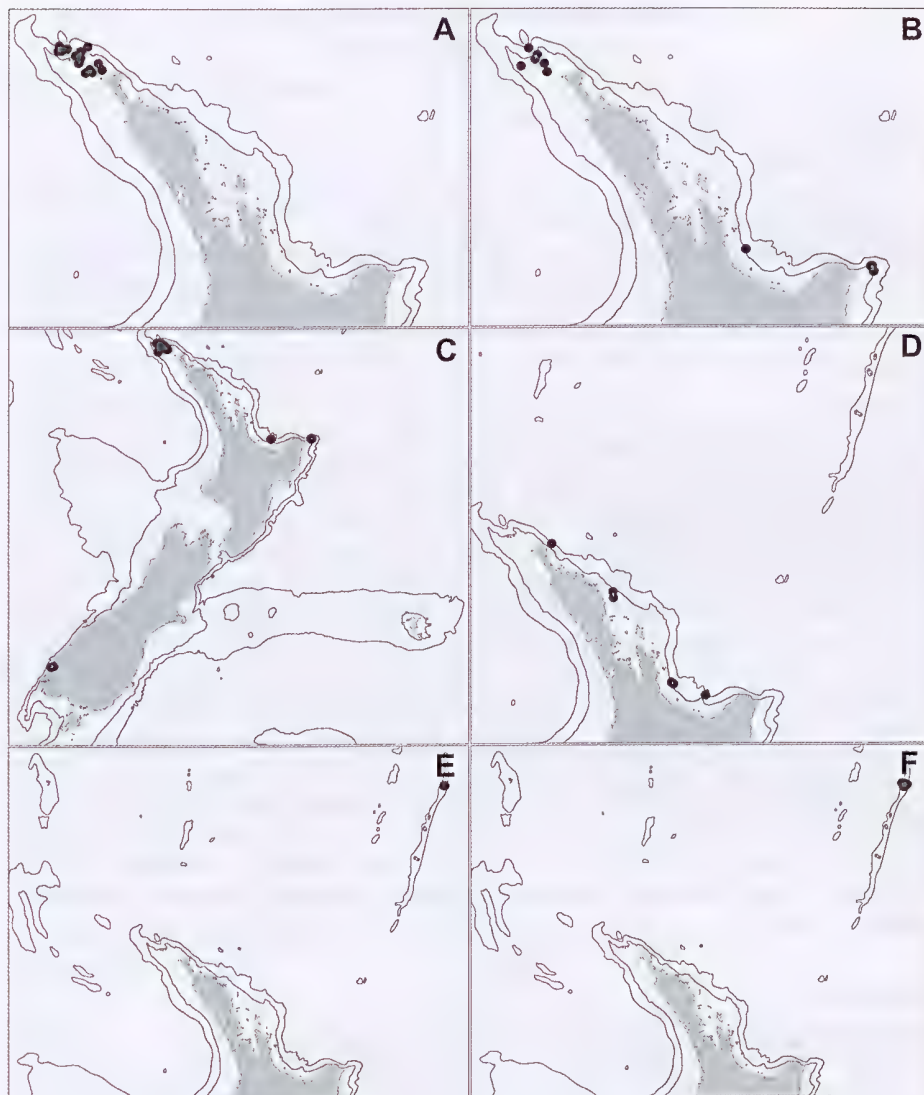


Fig. 15. Maps of the New Zealand region showing distributions of *Plectodon*, *Rhinoclama* (*s. str.*) and *Rhinoclama* (*Austroneara*) species (200 and 1000 m isobaths indicated). A, *Plectodon regalis* n. sp. B, *Rhinoclama* (*s. str.*) *aupouria* (Dell, 1950). C, *Rhinoclama* (*Austroneara*) *brevirostris* Powell, 1937. D, *Rhinoclama* (*Austroneara*) *finlayi* Powell, 1937. E, *Rhinoclama* (*Austroneara*) *raoulensis* Powell, 1958. F, *Rhinoclama* (*Austroneara*) *brooki* n. sp.

Remarks

Rhinoclama (*Austroneara*) *raoulensis* differs from *R. (A.) brevirostris* and *R. (A.) finlayi* principally in being shorter dorsoventrally and in having a less sharply defined angulation outside the posterodorsal margin. The gut of one specimen contained an ostracod and remains of two cumaceans (det. W. R. Webber, NMNZ). A second species from off Raoul Island is described below.

Rhinoclama (Austroneaera) brooki n. sp.

Figs 10D, 13F,H, 14A, 15F

Austroneaera raoulensis. – Brook & Marshall in Brook, 1998: 214 (in part not Powell, 1958).*Cuspidaria (Rhinoclama)* sp. 1 Spencer *et al.* (in press).*Material examined*

Holotype. SE of Nugent Island, Raoul Island, Kermadec Islands, New Zealand, 29°14.7'S, 177°49.4'W, 165–146 m, 28 Oct. 1975, RV *Acheron* (pr, M.152685).

Paratypes. Kermadec Islands. SE of Nugent Island, Raoul Island, 29°14.7'S, 177°49.4'W, 165–146 m, 28 Oct. 1975, RV *Acheron* (4v, M.225684). Off Raoul Island: NW of Fleetwood Bluff, 29°12.7'S, 177°56.1'W, 135 m (2v, M.225440); 29°13.0'S, 177°59.8'W, 201–146 m (1v, M.226915); E of Dayrell Islet, 29°14.73'S, 177°50.34'W, 135–146 m (1v, M.226672); SE of D'Arcy Point, 29°18.8'S, 177°54.2'W, 274–219 m (1v, M.226815); SE of Smith Bluff, 29°18.90'S, 177°56.40'W, 82–100 m (1v, M.227116).

Description

Shell up to 6.60 mm long, ovate-trigonal, thin, inflated, approximately 1.3× longer than high, translucent white, beaks distinctly opisthogyrous, anterior end 45%–50% of shell length, antero- and posterodorsal margins of right valve overlapping those of left. Prodissoconch approximately 170 µm wide, low, convex, smooth, no PII. Dissoconch anterior margin well rounded, smoothly merging with flat or very weakly convex anterodorsal margin and broadly convex ventral margin; posterodorsal margin more or less straight; posterior truncation weakly convex, oblique, corners tightly rounded. Right valve with two strong, well-defined anterior and posterior hinge teeth, posterior tooth considerably larger, length of inner dorsal margins weakly shelved to seat corresponding elevated narrow dorsal margins of left valve. Left valve edentulous. Resilifers sunken, narrowly ovate concave (lithodesma almost certainly present although absent from single valves). Interior with weak radial grooves, pallial line and large adductor scars well defined; pallial sinus broad, shallow, concave. Exterior convex, posterior area weakly flattened; posterodorsal margin of both valves margined by sharp angulation; sculptured with fine commarginal growth lines and extremely small, thinly distributed calcareous granules set in thin periostracum.

Distribution

Off Raoul Island, Kermadec Islands, 82–274 m (shells only; Fig. 15F).

Remarks

Rhinoclama (Austroneaera) brooki differs from *R. (A.) raoulensis* principally in attaining nearly twice the size (length up to 6.60 v. 3.80 mm), in having a more strongly convex ventral margin and in having a sharp exterior angulation bordering the posterodorsal margin. *Rhinoclama (A.) brooki* ranges deeper than *A. raoulensis* (82–174 v. 22–85 m). Specimens of *R. (A.) raoulensis* from 75–85 m, the deepest record for the species, were isolated valves (taken living at 22–45 m) and whether the two species have overlapping bathymetric ranges in life (syntopic?) remains to be established.

Etymology

After F. J. Brook (Whangarei), in appreciation of his work on Recent and fossil Mollusca of the Kermadec Islands (Brook 1998).

Rhinoclama (Austroneaera) tangaroa n. sp.

Figs 10F, 16A,C, 18A

Material examined

Holotype. Wanganella Bank, Norfolk Ridge, E slope, 32°35.3'S, 167°41.8'E, alive, 437–422 m, 29 Jan. 1981, RV *Tangaroa* (live taken: a right valve, left valve crushed; M.273140).

Paratypes. Same data as holotype (5v, M.234116).

Other material examined. SSE of Philip Island, Norfolk Island, 29°33'S, 168°07'E, 143 m (8v, M.225295); Middlesex Bank, NW of Three Kings Islands, 34°02.0'S, 171°44.0'E, 246–291 m (2v, M.151544).

Description

Shell up to 2.52 mm long, ovate–trigonal, beaks slightly anterior, thin and brittle, moderately inflated, 1.35× longer than high (holotype right valve), right valve slightly higher than left, fresh specimens strongly translucent apart from an opaque white band on interior against anterodorsal and posterodorsal margins. Prodissoconch approximately 200 µm wide, low, convex, smooth apart from fine commarginal wrinkles. Dissoconch anterior margin well rounded, smoothly merging with straight anterodorsal margin and broadly convex ventral margin; posterodorsal margin very broadly convex; posterior truncation weakly convex, more or less vertical, corners tightly rounded. Right valve with two well-defined anterior and posterior hinge teeth, posterior tooth larger, most of length of inner dorsal margins weakly shelved to seat corresponding elevated narrow dorsal margins of left valve. Left valve edentulous. Lithodesma stout (width 200 µm in holotype), about as long as wide, broadly rounded anteriorly, concave posteriorly; ligaments thin, narrowly ovate sunken resilifers concave. Pallial line and large adductor scars well defined; pallial sinus broadly concave. Exterior convex, posterior area flattened; sculptured with fine commarginal growth lines. Periostracum translucent, glossy, microscopic granules not evident.

Distribution

Norfolk Island, Wanganella Bank, and Middlesex Bank, 143–437 m; taken alive at 422–437 m (Fig. 18A).

Remarks

Rhinoclama (Austroneaera) tangaroa is extremely similar to *R. (A.) finlayi* in shape, but differs in attaining slightly smaller size (length up to 2.52 v. 3.50 mm), in lacking granular microsculpture and in having opaque white lines on the interior against the dorsal margins. The two well-preserved valves from Middlesex Bank (evidently a single individual) are indistinguishable from the Norfolk Ridge specimens.

Etymology

After RV *Tangaroa*.

Family SPHENIOPSIDAE Gardner, 1928

Diagnosis

Shell small (length up to 4 mm) subtrigonal, inequilateral or almost equilateral, equivalve, posterior end modestly produced or truncate, beaks median or posterior. Right valve with



Fig. 16. Shells of *Rhinoclama* (*Austroneaera*), *Rhinoclama* (*s. str.*) and *Grippina* species. A,C, *Rhinoclama* (*Austroneaera*) *tangaroa* n. sp.: holotype, right valve (A lower, C), length 2.10 mm (M.273140), and paratype, left valve, length 2.20 mm (M.234116), Wanganella Bank, Norfolk Ridge, 437–422 m (M.234116). B,D, *Rhinoclama* (*s. str.*) *aupouria* (Dell, 1950): left (B upper) and right valve, length 4.50 mm, right valve (D) length 4.40 mm, SE of Great Island, Three Kings Islands, 173–178 m (M.144427). E,G, *Grippina* *aupouria* (Powell, 1937): subadult, left (G upper), length 2.70 mm, 11 km NW of Great Island, Three Kings Islands, 310 m (M.93848). F,H, *Grippina* *aupouria*: adult, left (H upper) and right valve, length 3.50 mm, right valve (H lower) length 3.30 mm, Middlesex Bank, 201–216 m (M.93236).

anterior and posterior teeth, left valve without teeth; right valve teeth and left valve hinge line separated by wide gap occupied by lithodesma. Left valve without teeth. Pallial sinus shallow. Exterior with or without weak or strong commarginal ridges, some species with addition of minute punctae. Periostracum in some species set with minute calcareous granules. Dimyarian. Mantle margins fused, small pedal gape, two short conjoined siphons.

Genus *Grippina* Dall, 1912

Grippina Dall, 1912: 128. Type species (by original designation): *Grippina californica* Dall, 1912; Recent, California.

Remarks

Keen (1969a) referred *Grippina* to Spheniopsidae, which, until now, has been grouped in Heterodonta near Corbiculidae (Gardner 1928; Keen 1969a; Coan 1990b; Cosel 1995; Coan *et al.* 2000). However, *Grippina* species have sunken resiliifers and a lithodesma and some have exterior microsculpture extremely similar to that in some thraciids and cuspidariids, so it seems likely that the Spheniopsidae really belongs in Anomalodesmata (there seems no reason to doubt that *Grippina* and *Spheniopsis* are confamilial). Because shell shape and (when present) commarginal sculpture both suggest affinities with Cuspidariidae, I have tentatively grouped Spheniopsidae in Cuspidarioidea rather than Thracioidea pending knowledge of the anatomy.

Apart from some species of *Spheniopsis* Sandberger, 1861 from the Oligocene of Germany (Neuffer 1973), *S. americana* Dall, 1903 (Early Miocene, Florida) and the *Grippina* species reported below, the only other known spheniopsids are the Recent species *G. californica* Dall, 1912 (California), *S. frankbernardi* Coan, 1990 (Baja California and Costa Rica), *S. senegalensis* Cosel, 1995 (West Africa; Cosel 1995) and the three or four western Atlantic *Spheniopsis* species reported to E. V. Coan by the late D. R. Moore (Coan 1990b), one of which is *S. triquetra* (Verrill & Bush, 1898) (North Carolina). An undescribed *Spheniopsis* species is well represented in collections from bioclastic substrata off northern New Caledonia and Lifou, Loyalty Islands (MNHN). All the New Zealand *Grippina* species have extremely narrow geographic ranges, occur very patchily and most are rare relative to the volumes of sediment processed to recover them, which suggests they have unusually narrow ecological requirements. Spheniopsid diet is unknown, but if they are, indeed, cuspidariids, they are probably carnivores.

Coan (1990b) reported brooding in *G. californica*, the type species of the genus. The animal of an unspecified *Grippina* species was briefly described by Coan *et al.* (2000: 481): '... Dimyarian ... Mantle margins fused, with small pedal gape and two short conjoined siphons'.

Grippina aupouria (Powell, 1937)

Figs 10H, 14D, 16E–H, 18B, 21O

Mysella aupouria Powell, 1937a: 172, pl. 47, fig. 5; Powell, 1979: 395, fig. 98/4.

Grippina aupouria. – Coan, 1990b: 400.

Material examined

Syntypes. Off Three Kings Islands, New Zealand, 34°13.3'S, 172°12.0'E, 260 m, 17 Aug. 1932, RRS *Discovery II* (left and right v, BMNH 1962944).

Other material examined. Off Three Kings Islands: King Bank, 33°57.4'S, 172°19.4'E, 128–123 m (4v, M.148017); 18 km N of Great Island, 33°59.2'S, 172°13.6'E, 155 m (1v, M.93508); Three Kings Trough, 34°00'S, 171°55'E, 805 m (16v, M.17493); Middlesex Bank, 34°00.9'S, 171°44.7'E, 201–216 m (3pr, 4v, M.93236); 34°01'S, 172°07'E, 622 m (3v, M.34959); Middlesex Bank, 34°01.2'S, 171°44.4'E, 206–211 m (1v, M.148108); 13 km N of Great Island, 34°01.8'S, 172°12.0'E, 508 m (2v, M.149721); Middlesex Bank, 34°02.0'S, 171°44.0'E, alive, 246–291 m (7pr, 23v, M.148023); Middlesex Bank, 34°02.1'S, 171°45.8'E, 221–206 m (1pr, 2v, M.148021); 24 km NW of Great Island, 34°05.9'S, 171°55.1'E, alive, 710 m (1pr, 5v, M.94378); 11 km NW of Great Island, 34°06.5'S, 172°04.7'E, alive, 310 m (3pr, 8v, M.93848); off North-east Island, 34°08.5'S, 172°11'E, 102 m (2pr, 3v, M.34536); 34°10'S, 172°12'E, 252

m (1v, M.34199); S of Great Island, 34°14.1'S, 172°09.0'E, alive, 192–202 m (1pr, 15v, M.148019); 39 km SW of Great Island, 34°17.6'S, 171°45.3'E, 427 m (1v, M.94288). NW of Cape Reinga, 34°14.2'S, 172°32.4'E, 100 m (2pr, M.94554).

Description

Shell up to 4.15 mm long, obliquely ovate-trigonal, of moderate thickness, rather strongly inflated, large individuals up to 1.26× longer than high, with increasing shell size anterior end elongating anteroventrally more rapidly than posterior so that beak position shifts from an initial position slightly behind midlength to approximately posterior one-third (increasingly inequilateral); fresh specimens semitranslucent white with small, sparse, irregular, cuneiform, opaque white radial streaks. Prodissoconch approximately 270 µm wide, prominent, globular, smooth; PI approximately 230 µm wide. Dissoconch anterior margin well rounded, smoothly merging with more or less straight anterodorsal margin and broadly rounded ventral margin, posterodorsal margin broadly rounded; posterior truncation short, straight, oblique, extremities roundly angulate. Right valve with two strong, well-defined hinge teeth that gently converge inwards relative to valve margins, separated by very broad space occupied by lithodesma, anterior tooth longer, inner anterodorsal margin shelved to seat corresponding elevated narrow margin of left valve. Left valve with small rounded process on anterior corner of lithodesma space and shallow groove posteriorly that seats dorsal part of posterior right valve tooth, lithodesma space oblique and narrower than in right valve. Lithodesma stout, anteriorly tapered, subtrigonal in dorsal view, ligaments thin, sunken resilifers shallowly concave, 500 µm wide in a shell 3.20 mm long. Interior glossy apart from opaque white patches near anterodorsal and posterodorsal margins; ventrally enlarging groove extending gently posteriorly from below umbones, ending as an oblique pit; pallial line and large adductor scars well defined; pallial sinus shallow, concave. Exterior convex, posterior end flattened, sculptured with low rounded commarginal ridges; and a crisp microsculpture of crowded, flat-topped, calcareous periostracal granules, some of which are connected in groups of two to four that are aligned commarginally.

Distribution

Off Three Kings Islands, 98–805 m; taken alive at 98–710 m from comminuted bryozoan/shell substrata. Restricted endemic (Fig. 18B).

Remarks

Originally described in the montacutid genus *Mysella* Angas, 1877, this species was referred to *Grippina* by Coan (1990b) because of similarity to the type species in shape, size, thickness, sculpture, hinge morphology, pallial line and muscle scars. Six additional New Zealand *Grippina* species are described below.

Grippina rex n. sp.

Figs 10I, 14E, 17A,C, 18C

Grippina sp. 7 Spencer *et al.* (in press).

Material examined

Holotype. Off Three Kings Islands, New Zealand, 34°11'S, 172°10'E, alive, 91 m, 19 Feb. 1974, RV *Acheron* (pr, M.33807).

Paratypes. Off Three Kings Islands: Middlesex Bank, 33°57.0'S, 171°45.4'E, alive, 98–103 m (3pr, M.148022); King Bank, 33°57.4'S, 172°19.4'E, 128–123 m (2v, M.149514); Three Kings Trough, 34°00'S,

171°55'E, 805 m (5v, M.149518); Middlesex Bank, 34°01.2'S, 171°44.4'E, 206–211 m (1v, M.149517); Middlesex Bank, 34°02.0'S, 171°44.0'E, 246–291 m (9v, M.149512); 11 km NW of Great Island, 34°06.5'S, 172°04.7'E, 310 m (1v, M.149516); off North-east Island, 34°08.5'S, 172°11'E, 102 m (2v, M.149513).

Description

Shell up to 5.10 mm long, obliquely ovate-trigonal, of moderate thickness, rather strongly inflated, large individuals up to 1.44× longer than high, with increasing shell size anterior end elongating anteroventrally slightly more rapidly than posterior so that beak position shifts from an initial position in front of posterior one-third to behind it; fresh specimens semitranslucent white with small, irregular, cuneiform, opaque white radial streaks. Prodissoconch approximately 230 µm wide, prominent, smooth; PI approximately 200 µm wide, globular. Dissoconch anterior margin well rounded, smoothly merging with more or less straight anterodorsal margin and broadly rounded ventral margin, posterodorsal margin broadly rounded or almost straight; posterior truncation short, straight, oblique, extremities roundly angulate. Right valve with two strong, well defined hinge teeth that converge inwards relative to margins, posterior tooth at a markedly higher angle than anterior; separated by very broad space occupied by lithodesma, anterior tooth longer, inner anterodorsal margin shelved to seat corresponding elevated narrow dorsal margin of left valve. Left valve with increasingly prominent rounded process on anterior corner of lithodesma space and concave space posteriorly that seats posterior right valve tooth, lithodesma space oblique and narrower than in right valve. Lithodesma stout (width 570 µm in adult), anteriorly tapered, subtrigonal in dorsal view, ligaments thin, sunken resilifers shallowly concave. Interior glossy; ventrally enlarging groove extending gently posteriorly from below umbones, ending as an oblique pit; pallial line and large adductor scars well defined, pallial sinus shallow, concave. Exterior convex, posterior end flattened; with a crisp microsculpture of crowded, flat-topped, calcareous periostracal granules, many of which are grouped in pairs aligned commarginally.

Distribution

Off Three Kings Islands, 91–805 m; taken alive at 91–103 m from comminuted bryozoan/shell substrata. Restricted endemic (Fig. 18C).

Remarks

Compared with the sympatric species *G. aupouria*, which has a similar pattern of white radial streaks, *G. rex* differs in attaining larger size, in that the anterior end increases in length more slowly relative to the posterior with increasing shell size and the posterior tooth on the left valve is inclined at a steeper angle to the valve margin. *Grippina rex* differs further in having a stronger process on the left valve hinge, stronger microsculpture and in lacking commarginal ridges.

Etymology

From the Latin *rex* (king).

Grippina punctata n. sp.

Figs 10J, 14F, 17B,D, 18D

Grippina sp. 2 Spencer *et al.* (in press).*Material examined*

Holotype. Off Spirits Bay, New Zealand, 34°19.98'S, 172°45.79'E, 63 m, 25 Jan. 1999, RV *Kaharoa* (pr, M.152679).

Paratypes. Off Three Kings Islands: 37 km NE of Great Island, 33°58.0'S, 172°30.6'E, 550 m (4v, M.149724); Three Kings Trough, 34°00'S, 171°55'E, 805 m (18v, M.149521); 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (1pr, M.149601); outer South-east Bay, Great Island, 34°10'S, 172°08'E, 55 m (4v, M.33965); S of Great Island, 34°14.1'S, 172°09.0E, alive, 192–202 m (1pr, M.149520). Off Spirits Bay, 34°18.36'S, 172°49.39'E, alive, 68 m (3pr, many v, M.149508); 34°19.98'S, 172°45.79'E, 63 m (20v, M.149509); 34°21.60'S, 172°43.19'E, alive, 48 m (2pr, 3v, M. 153097). NW of Cape Maria van Diemen, 34°20.0'S, 172°30.0'E, 100 m (1v, M.93740).

Other material examined. Off Spirits Bay, 34°21.15'S, 172°45.92'E, 54 m (7v, M.154153). NNE of Cape Reinga, 34°22.47'S, 172°42.08'E, 53 m (1pr, 1v, M.152031).

Description

Shell up to 2.15 mm long, obliquely ovate-trigonal, thick to very thick, strong, moderately inflated, up to 1.32× longer than high, posterior end occupying approximately 36% of shell length, fresh specimens semitranslucent white. Prodissoconch approximately 220 µm wide, convex, topographically complex, minutely maleate and wrinkled, PI approximately 200 µm wide. Dissoconch anterior margin well rounded, smoothly merging with broadly rounded or almost flat anterodorsal margin and broadly rounded ventral margin, posterodorsal margin broadly rounded or straight; posterior truncation short, typically broadly concave, straight in few specimens, oblique, extremities angulate. Right valve with two strong, well-defined hinge teeth, both gently converging inwards relative to valve margins or posterior tooth more or less parallel to margin, separated by very broad space occupied by lithodesma (present but lost), inner anterodorsal margin shelved almost to anterior extremity to seat corresponding elevated narrow dorsal margin of left valve. Left valve with indentations that seat dorsal parts right valve teeth, lithodesma space smaller than in right valve. Resilifers sunken, narrowly ovate, oblique. Interior glossy, shallow groove extending gently posteriorly from below umbones, pallial line and large adductor scars well defined; pallial sinus shallow, concave. Exterior convex, posterior end flattened, valves up to approximately 700 µm length sculptured with deep circular pits arranged commarginally, thereafter with low, broad, rounded commarginal ridges and a crisp microsculpture of densely crowded, flat-topped, calcareous periostracal granules that are grouped in more or less commarginal rows.

Distribution

Off Three Kings Islands and of northern tip of Northland, 53–805 m; taken alive at 48–202 m from comminuted bryozoan/shell and sand substratum (Fig. 18D).

Remarks

Grippina punctata differs from *G. aupouria* and *G. rex* principally in attaining smaller size, in being much thicker, in having a projecting boss on the prodissoconch, in having a



Fig. 17. Shells of *Grippina* species. *A,C*, *Grippina rex* n. sp., holotype, left (*A* upper) and right valve, length 4.10 mm, off Three Kings Islands, 91 m (M.33807). *B,D*, *Grippina punctata* n. sp.: holotype, left (*B* upper) and right valve, length 1.45 mm, off Spirits Bay, 63 m (M.152679). *E,G*, *Grippina globosa* n. sp.: holotype, right valve (*E,G* lower), length 1.30 mm (M.152672), and paratype, left valve (M.149490), Middlesex Bank, NW of Three Kings Islands, 246–291 m. *F,H*, *Grippina spirata* n. sp.: holotype, left (*F* upper) and right valve, length 2.10 mm, off Spirits Bay, 63 m (M.149519).

(typically) concave instead of straight posterior truncation, in having pits on the early dissoconch and in lacking opaque white radial streaks.

Etymology

From the Latin *punctatus* (pricked with small holes).

Grippina globosa n. sp.

Figs 10K,L, 17E,G, 18E, 21P

Grippina sp. 3 Spencer *et al.* (in press).*Material examined*

Holotype. Middlesex Bank, NW of Three Kings Islands, New Zealand, 34°02.0'S, 171°44.0'E, alive, 246–291 m, 31 Jan. 1981, RV *Tangaroa* (1v, M.152672).

Paratypes. 37 km NE of Great Island, Three Kings Islands, 33°58.0'S, 172°30.6'E, 550 m (1v, M.149723). Middlesex Bank, NW of Three Kings Islands, 34°02.0'S, 171°44.0'E, alive, 246–291 m (2pr, 3v, M.149490). 37 km NW of Great Island, 34°02.0'S, 171°48.4'E, 188 m (1pr, M.150078). NW of Cape Reinga, 34°14.2'S, 172°32.4'E, 100 m (1pr, M.94549).

Description

Shell up to 1.43 mm long, obliquely ovate-trigonal, of moderate thickness, strongly inflated, up to 1.18× longer than high, posterior end occupying approximately 38% of shell length, fresh specimens semitranslucent white. Prodissoconch approximately 400 µm wide, broadly convex, smooth, PI approximately 200 µm wide. Dissoconch anterior margin well rounded, smoothly merging with broadly rounded anterodorsal and ventral margins, posterodorsal margin almost straight; posterior truncation short, very weakly convex, oblique, extremities roundly angulate. Right valve with two strong, well-defined hinge teeth that are separated by a broad space occupied by lithodesma and small boss in front of posterior tooth; inner anterodorsal margin shelved to seat corresponding elevated narrow dorsal margin of left valve. Left valve with rather deep indentations that seat dorsal sides of right valve teeth, depth of indentations effectively forming small anterior and posterior teeth bordering space occupied by lithodesma. Lithodesma stout (width 170 µm in adult holotype), about as long as wide, anteriorly tapered, subtrigonal in dorsal view, ligaments thin, sunken resilifers shallowly concave. Interior glossy, shallow groove extending gently posteriorly from below umbones, pallial line and large adductor scars well defined; pallial sinus shallow, concave. Exterior convex, posterior end flattened, sculptured throughout with fine commarginal growth lines; minute, crowded pits on early dissoconch, no calcareous periostracal granules.

Distribution

Off Three Kings Islands, 100–550 m from comminuted bryozoan/shell substratum; taken alive at 246–291 m (Fig. 18E).

Remarks

Grippina globosa is much smaller than previously described *Grippina* species and is further distinguished by the depressed, relatively large prodissoconch, the strongly convex dissoconch, the short anterior end and the presence of a boss in front of the posterior tooth on the right valve.

Grippina sp. 5 of Spencer *et al.* (in press) from off the Three Kings Islands at 805 m, is very similar to *G. globosa* in shape, but larger and with a considerably broader prodissoconch. Regrettably, the only known specimen, a single valve, was lost during preparation for scanning electron microscopy.

Etymology

From the Latin *globosus* (spherical).

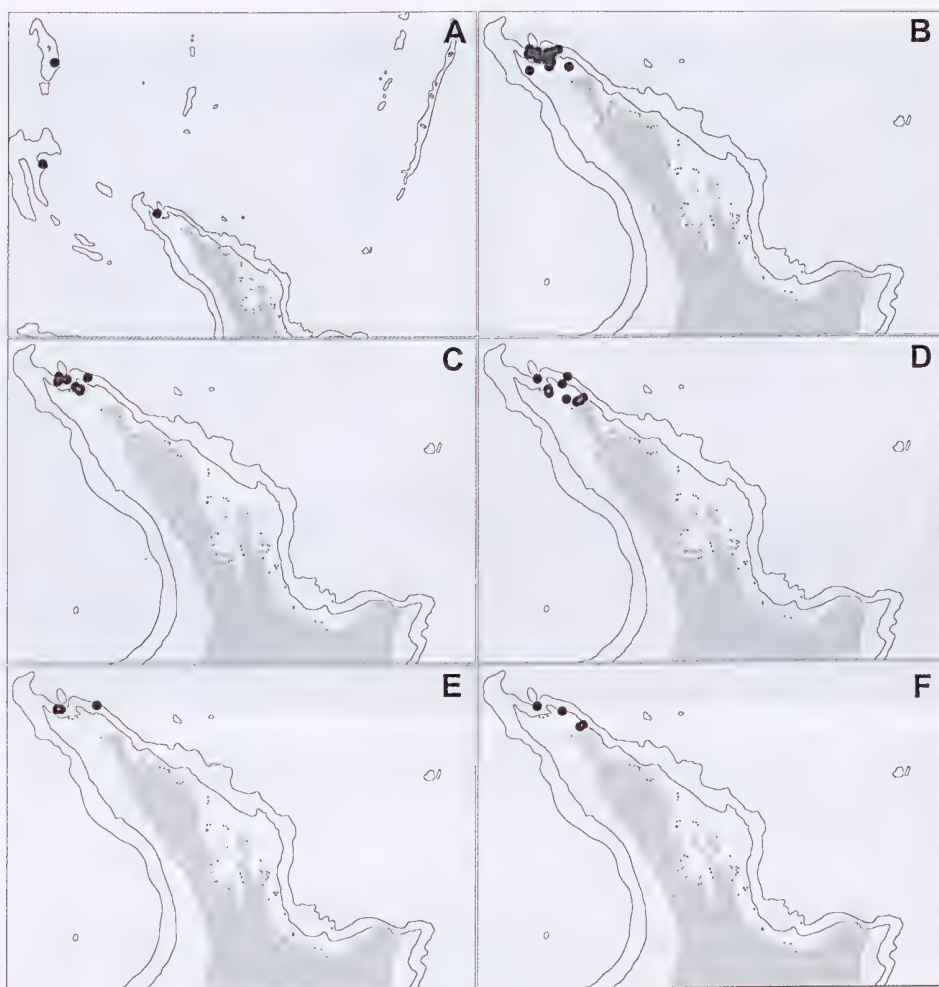


Fig. 18. Maps of the New Zealand region showing distributions of *Rhinoclama* (*Austroneaera*) and *Grippina* species (200 and 1000 m isobaths indicated). A, *Rhinoclama* (*Austroneaera*) *tangaroa* n. sp. B, *Grippina* *aupouria* (Powell, 1937). C, *Grippina* *rex* n. sp. D, *Grippina* *punctata* n. sp. E, *Grippina* *globosa* n. sp. F, *Grippina* *spirata* n. sp.

***Grippina spirata* n. sp.**

Figs 10M, 14G, 17F,H, 18F

Grippina sp. 6 Spencer *et al.* (in press).

Material examined

Holotype. Off Spirits Bay, New Zealand, 34°19.98'S, 172°45.79'E, alive, 63 m, 25 Jan. 1999, RV *Kaharoa* (pr, M.149519).

Paratypes. Three Kings Islands, 22 km ENE of Great Island, 34°05.0'S, 172°24.6'E, 200 m (1pr, M.149602). Off Spirits Bay, 34°18.36'S, 172°49.39'E, 68 m (4v, M.149522).

Description

Shell up to 2.05 mm long, obliquely ovate-trigonal, of moderate thickness, strong, moderately inflated, up to 1.46× longer than high, posterior end occupying approximately

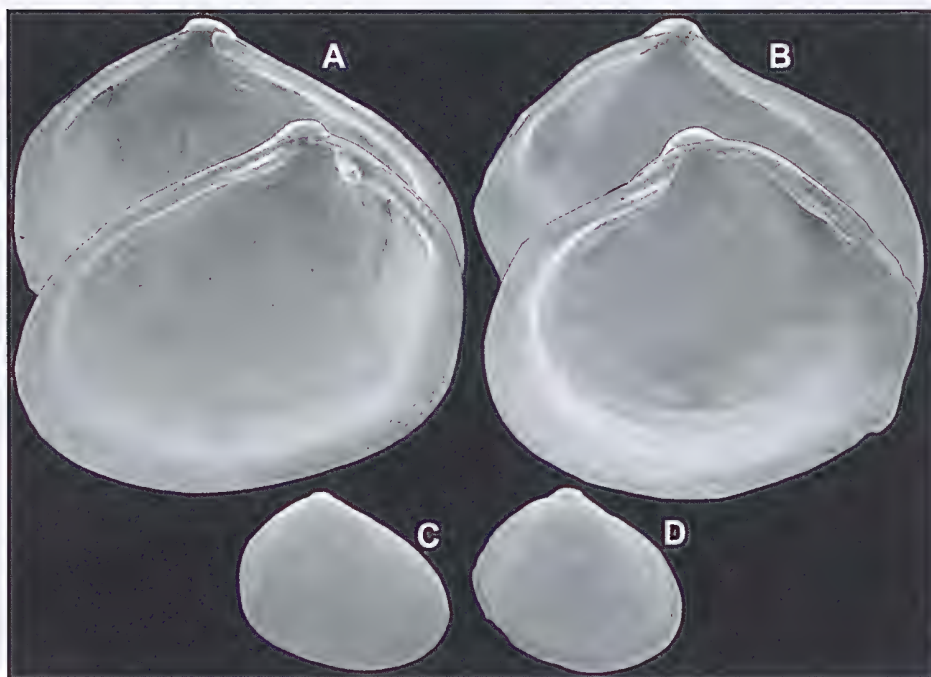


Fig. 19. Shells of *Grippina* species. *A,C*, *Grippina acherontis* n. sp.: holotype, left (*A* upper) and right valve, length 2.20 mm, off Patea, 40 m (M.152680). *B,D*, *Grippina pumila* n. sp.: holotype, left (*B* upper) and right valve, length 1.45 mm, off Puysegur Point, 183 m (M.152677).

34% of shell length, fresh specimens semitranslucent white. Prodissoconch approximately 230 μm wide, prominent, globose, smooth, PI approximately 200 μm wide. Dissoconch anterior margin well rounded, smoothly merging with very broadly rounded anterodorsal and ventral margins, posterodorsal margin almost straight; posterior truncation short, oblique, concave, extremities angulate. Right valve with two strong, well-defined hinge teeth, anterior tooth longer, separated by very broad space occupied by lithodesma, inner anterodorsal margin shelved to seat corresponding elevated narrow dorsal margin of left valve. Left valve with shallow posterior indentation that seats dorsal part of right valve posterior tooth, lithodesma space smaller than in right valve. Lithodesma stout (lost), subrectangular, ligaments thin, sunken resilifers shallowly concave. Interior glossy, smooth, pallial line and large adductor scars well defined; ventrally enlarging groove extending gently posteriorly from below umbones, ending as an oblique pit; pallial sinus shallow, broadly concave. Exterior convex, posterior end shallowly concave, sculptured with low, rounded commarginal ridges, and a microsculpture of densely crowded, flat-topped, mostly elongate, calcareous periostracal granules that are aligned commarginally.

Distribution

East of Three Kings Islands and off Spirits Bay, 63–200 m; taken alive at 63 m from comminuted shell and sand substratum (Fig. 18F).

Remarks

Grippina spirata resembles *G. punctata* in gross facies, but differs markedly in having a smoothly convex prodissoconch and in lacking punctations on the early dissoconch. The two species are sympatric. *Grippina spirata* differs principally from *G. aupouria* and *G. rex* in attaining smaller size, in lacking white radial streaks and in details of exterior microsculpture and differs from *G. globosa* in details of shape, size, hinge morphology and sculpture.

Etymology

From the type locality, Spirits Bay.

Grippina acherontis n. sp.

Figs 10*N*, 14*H*, 19*A*, *C*, 20*A*, 21*Q*

Grippina sp. 1 Spencer *et al.* (in press).

Material examined

Holotype. S of Patea, New Zealand, 39°56'S, 174°26'E, alive, 40 m, 2 Mar. 1976, RV *Acheron* (pr. M.152680).

Paratypes. Same data as holotype (22pr, M.53594).

Description

Shell up to 2.45 mm long, obliquely ovate-trigonal, of moderate thickness, moderately inflated, up to 1.32× longer than high, anterior end becoming somewhat longer relative to anterior with increasing shell size, posterior end occupying up to 35% of shell length in adults, fresh specimens semitranslucent white. Prodissoconch approximately 270 µm wide, prominent, broadly convex, smooth, PI approximately 230 µm wide. Dissoconch anterior margin well rounded, smoothly merging with more or less straight anterodorsal margin and broadly rounded ventral margin, posterodorsal margin very broadly rounded; posterior truncation short, straight, oblique, extremities roundly angulate. Right valve with two strong, well-defined hinge teeth, anterior tooth longer, posterior tooth more prominent, separated by very broad space occupied by lithodesma, inner anterodorsal margin shelved to seat corresponding elevated narrow dorsal margin of left valve. Left valve with small boss at posterior end of elevated dorsal margin, lithodesma space smaller than in right valve. Lithodesma stout (width 320 µm in adult), subrectangular in dorsal view, ligaments thin, sunken resilifers shallowly concave. Interior glossy, smooth, pallial line and large adductor scars well defined, pallial sinus shallow, concave. Exterior convex, posterior end flattened, with low, very weak, rounded commarginal ridges; and a crisp microsculpture of crowded, flat-topped, calcareous periostracal granules that are grouped in commarginal rows.

Distribution

Off Patea, south-western North Island, 40 m, living in clean sand (Fig. 20*A*).

Remarks

Grippina acherontis most closely resembles *G. aupouria* in gross facies, but differs in attaining smaller size, in lacking opaque white radial streaks and in that the beaks in adults are more posterior than in subadults of *G. aupouria* of the same size.

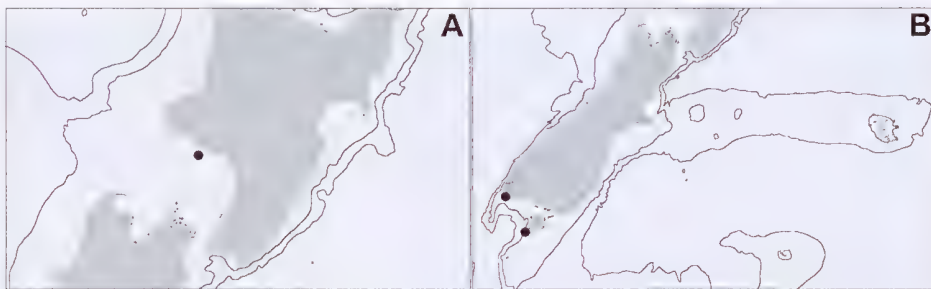


Fig. 20. Maps of the New Zealand region showing distributions of *Grippina* species (200 and 1000 m isobaths indicated). A, *Grippina acherontis* n. sp. B, *Grippina pumila* n. sp.

Etymology

After RV *Acheron* from which the type material was dredged.

Grippina pumila n. sp.

Figs 10O, 14I, 19B,D, 20B, 21R

Grippina sp. 4 Spencer *et al.* (in press).

Material examined

Holotype. Off Puysegur Point, New Zealand, 46°11'S, 166°30'E, 183 m, Dec. 1908, SS *Rakiura* (pr, M.152677).

Paratypes. Off Puysegur Point, New Zealand, 46°11'S, 166°30'E, 183 m, Dec. 1908, SS *Rakiura* (16v, M.143883). Off Poutama Island, Big South Cape Island, Stewart Island, 47°16'S, 167°23'E, 55 m (1pr, 36v, M.63606).

Description

Shell up to 2.80 mm long, obliquely ovate-trigonal, of moderate thickness, moderately inflated, approximately 1.2× longer than high; umbones at approximately mid-shell length in specimens less than approximately 1.60 mm long, anterior end elongating to varying degrees in larger specimens so that umbones are at approximately the posterior one-third of shell length in adults, fresh specimens semitranslucent white. Prodissoconch approximately 270 µm wide, prominent, broadly convex, topographically complex, PI approximately 230 µm wide. Dissoconch anterior margin well rounded, smoothly merging with more or less straight anterodorsal margin and broadly rounded ventral margin, posterodorsal margin broadly rounded; posterior truncation short, straight, oblique, extremities roundly angulate. Right valve with two strong, well-defined hinge teeth, anterior tooth longer, posterior tooth more prominent, separated by very broad space occupied by lithodesma, inner anterodorsal margin shelved to seat corresponding elevated narrow dorsal margin of left valve. Left valve with small boss at posterior end of elevated anterodorsal margin (pseudocardinal), lithodesma space smaller than in right valve. Lithodesma stout (width 170 µm in holotype), about as long as broad, ligaments thin, sunken resilifers shallowly concave. Interior glossy, smooth, pallial line and large adductor scars well defined, pallial sinus shallow, concave. Exterior convex, posterior area flattened. Sculptured with low, rounded irregular commarginal ridges and incised growth lines; no calcareous periostracal granules.

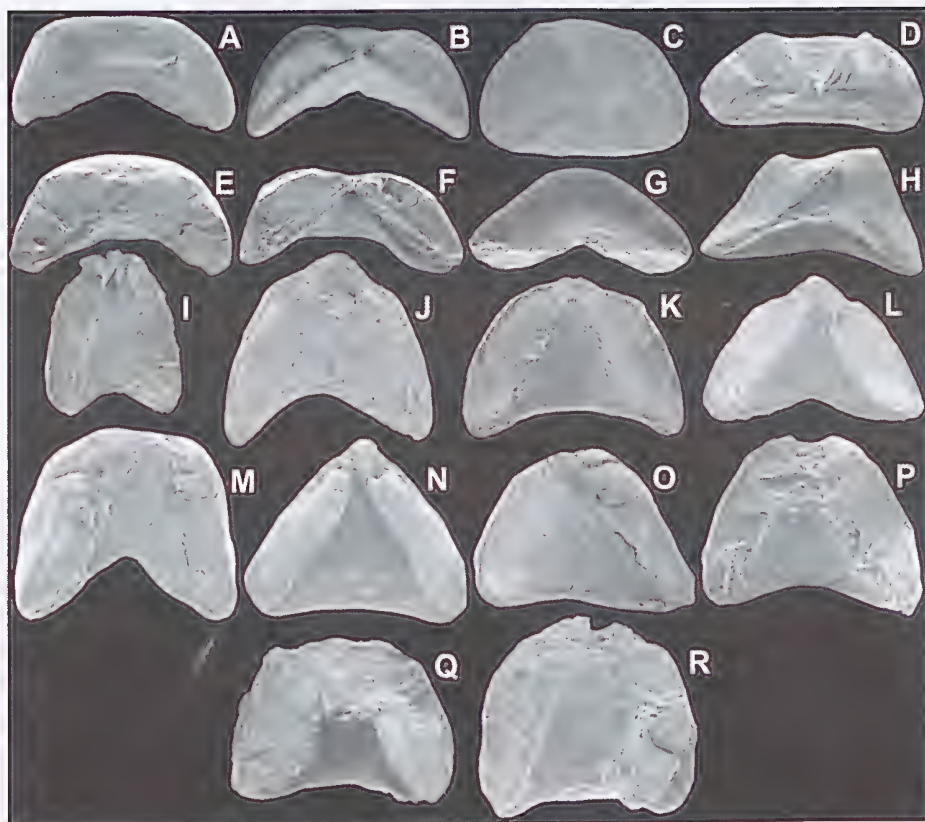


Fig. 21. Lithodesmas of Thraciidae, Myochamidae, Cuspidariidae and Spheniopsidae. *A*, *Thracia* (*Odoncinea*) *vitrea* (Hutton, 1873), width 1.00 mm, ex shell 15.0 mm long, Manaroa Bay, Pelorus Sound, 5–18 m (M.144402). *B*, *Asthenothaerus maxwelli* n. sp., width 6.45 mm, ex holotype 30.5 mm long, Horseshoe Bay, Stewart Island (M.152678). *C*, *Barythaerus biconvexus* (Powell, 1927), width 0.23 mm, ex shell 2.00 mm long, off Poutama Island, Big South Cape Island, Stewart Island, 55 m (M.19878). *D*, *Barythaerus cuneatus* (Powell, 1937), width 0.48 mm, ex shell 3.20 mm long, off Spirits Bay, 68 m (M.149504). *E*, *Parvithracia* (s. str.) *suteri* (Finlay, 1927), width 0.40 mm, ex shell 3.42 mm long, North Arm, Port Pegasus, Stewart Island, 37–44 m (M.44790). *F*, *Parvithracia* (s. str.) *ampla* n. sp., width 0.90 mm, ex holotype 6.60 mm long, Saunders Canyon, off Otago Peninsula, 457 m (M.9125). *G*, *Parvithracia* (*Pseudoasthenothaerus*) *fragilissima* n. sp., width 0.87 mm (face down), ex holotype 6.70 mm long, Challenger Plateau, 1005–1009 m (NZOI H-808). *H*, *Hunkydora novozelandica* (Reeve, 1859), width 1.65 mm, ex shell 11.2 mm long, off point SW of Munro Bay, Whangarei Harbour, 7–10 m (M.152673). *I*, *Pseudogrippina wangellicca* n. sp., width 0.23 mm ex holotype 2.30 mm long, Wanganella Bank summit, Norfolk Ridge, 113 m (M.152681). *J*, *Plectodon lepidus* n. sp., width 0.50 mm, ex holotype 5.25 mm long, off E side of Mayor Island, 59–74 m (M.152682). *K*, *Plectodon regalis* n. sp., width 0.57 mm, ex holotype 5.20 mm long, off Three Kings Islands, 91 m (M.152684). *L*, *Austroneaera brevirostris* Powell, 1937, width 0.40 mm, ex shell 3.70 mm long, SE of Great Island, 173–178 m (M.144426). *M*, *Austroneaera raoulensis* Powell, 1958, width 0.30 mm, ex shell 3.20 mm long, off Meyer Island, Raoul Island, Kermadec Islands, 27–22 m (M.225814). *N*, *Rhinoclama aupouria* (Dell, 1950), width 0.48 mm, ex shell 4.40 mm long, SE of Great Island, Three Kings Islands, 173–178 m (M.144427). *O*, *Grippina aupouria* (Powell, 1937), width 0.50 mm, ex shell 3.20 mm long, Middlesex Bank, NW of Three Kings Islands, 246–291 m (M.148023). *P*, *Grippina globosa* n. sp., width 0.17 mm, ex holotype 1.30 mm long, Middlesex Bank, 246–291 m (M.152672). *Q*, *Grippina acherontis* n. sp., width 0.32 mm, ex holotype 2.20 mm long, off Patea, 40 m (M.152680). *R*, *Grippina pumila* n. sp., width 0.17 mm, ex holotype 1.45 mm long, off Puysegur Point, 183 m (M.152677).

Distribution

Off Puysegur Point, south-western South Island, and southern Stewart Island, 55–183 m; taken alive at 183 m from comminuted bryozoan/shell substratum (Fig. 20B).

Remarks

Grippina pumila resembles *G. punctata* in having a topographically complex prodissoconch, but differs from that and all other *Grippina* species from the New Zealand region other than *G. globosa* in lacking granulate microsculpture. *Grippina pumila* differs from the allopatric species *G. globosa* in attaining larger size and in various details of shape and sculpture.

Etymology

From the Latin *pumilus* (small).

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How many species of *Hexabranchnus* (Opisthobranchia : Dorididae) are there?

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Abstract

Anatomical examination of several specimens of *Hexabranchnus*, collected from the extreme boundaries of its geographic range and other localities, revealed that there are two distinct species within this genus. One of these species is widely distributed throughout the tropical Indo-Pacific. The oldest available name for the Indo-Pacific species is *Hexabranchnus lacer* (Cuvier, 1804). The study of the original type material of *H. lacer* confirmed that it is a senior synonym of other names introduced subsequently, including *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830), which is the name most commonly used for this species. However, according to the provisions of the International Code of Zoological Nomenclature (Article 23.9.1), the name *H. sanguineus* has precedence over *H. lacer*, which has never been used as valid, except for the original description. *Hexabranchnus praetextus* Ehrenberg, 1828 is also a senior synonym of *H. sanguineus* that has not been used as valid since its original description and it is also invalidated under the provisions of Article 23.9.1.

The other species, *Hexabranchnus morsomus* Ev. Marcus & Er. Marcus, 1962, appears to be endemic to the Caribbean Sea. *Hexabranchnus sanguineus* and *H. morsomus* are clearly distinguishable by the morphology of the reproductive system and the radula. Hypotheses on the speciation process that took place in *Hexabranchnus*, the possible origin of the two species and the geographic range of the genus are discussed.

Introduction

A number of species belonging to genus *Hexabranchnus* have been described from the tropical Indo-Pacific (Table 1). Most of these nominal species had been distinguished, when originally introduced, by differences in the colour pattern. Eliot (1910) suggested that it was highly probable that all the common species of *Hexabranchnus* were varieties of the same species, with the possible exception of *Hexabranchnus adamsii* Gray, 1850. He commented that the valid name for the most common Indo-Pacific species was probably *Hexabranchnus marginatus* (Quoy & Gaimard, 1832). Since then, a few more species of *Hexabranchnus* have been introduced. Ostergaard (1955) described *Hexabranchnus aureomarginatus* and *H. tinkeri* from Hawaii. Marcus and Marcus (1962) agreed in considering all the Indo-Pacific species as synonyms but, at the same time, described the new species, namely *H. morsomus*, from the Caribbean Sea. These authors justified the introduction of a new species of this genus based on morphological differences and the geographic isolation of the Caribbean.

Steps towards the synonymisation of all species of *Hexabranchnus* were taken up again by Gohar and Soliman (1963), who illustrated the colour variation within *Hexabranchnus sanguineus* in a small geographic area in the Red Sea. More recently, Thompson (1972) argued that the colour pattern of the species of *Hexabranchnus* is extremely variable and regarded all the Indo-Pacific species as synonyms (including *H. aureomarginatus* and *H. tinkeri*), but he did not provide anatomical evidence to sustain this conclusion. Regarding *H. morsomus*, Thompson (1972) stated that there are no compelling reasons to separate it from the Indo-Pacific species besides the geographic range and small radular differences, and regarded both species as synonyms. In addition, Thompson (1972)

Table 1. Available species names introduced for Indo-Pacific species of *Hexabranchnus*, including authorship, publication date and type localityNames marked with an asterisk have been synonymized with *H. sanguineus* by Thompson (1972)

| Species name | Type locality |
|--|-----------------------------|
| <i>Doris lacera</i> Cuvier, 1804 | Timor |
| * <i>Hexabranchnus praetextus</i> Ehrenberg, 1828 | El Tûr, Egypt (Red Sea) |
| <i>Doris sanguinea</i> Rüppell & Leuckart, 1830 | El Tûr, Egypt (Red Sea) |
| * <i>Doris flammulata</i> Quoy & Gaimard, 1832 | Tonga |
| * <i>Doris marginata</i> Quoy & Gaimard, 1832 | Amboina |
| <i>Heptabranchnus burnetti</i> A. Adams, 1848 | Borneo |
| <i>Hexabranchnus adamsii</i> J. E. Gray, 1850 | Borneo |
| <i>Hexabranchnus sandwichensis</i> J. E. Gray, 1850 | Hawaii |
| * <i>Doris cardinalis</i> Gould, 1852 | Honolulu, Hawaii |
| <i>Doris sumptuosa</i> Gould, 1852 | Tonga |
| <i>Doris superba</i> Gould, 1852 | Tutuilla, Samoa |
| <i>Doris cardinalis</i> Gould, 1852 | Honolulu, Hawaii |
| * <i>Doris sandwichiensis</i> Souleyet, 1852 | Hawaii |
| <i>Doris gloriosa</i> Kelaart, 1858 | Tricomalie, Sri Lanka |
| * <i>Hexabranchnus pulchellus</i> Pease, 1860 | Hawaii |
| * <i>Hexabranchnus suezensis</i> Abraham, 1876 | Red Sea |
| * <i>Hexabranchnus pellucidulus</i> Abraham, 1876 | Unknown |
| <i>Aethedoris indica</i> Abraham, 1877 | Madras, India |
| * <i>Hexabranchnus aneiteumensis</i> Abraham, 1877 | Aneiteum, New Hebrides |
| * <i>Hexabranchnus mauritiensis</i> Abraham, 1877 | Mauritius |
| * <i>Hexabranchnus orbicularis</i> Abraham, 1877 | Mauritius |
| * <i>Hexabranchnus anaiteus</i> Bergh, 1878 | New Hebrides |
| <i>Hexabranchnus faustus</i> Bergh, 1878 | Aibukit, Palau |
| <i>Hexabranchnus notatus</i> Bergh, 1878 | Tonga |
| <i>Hexabranchnus petersi</i> Bergh, 1878 | Mozambique |
| * <i>Albania formosa</i> Collingwood, 1881 | Ke Lung, Taiwan |
| * <i>Doris imperialis</i> Kent, 1897 | Abrolhos Islands |
| * <i>Hexabranchnus digitatus</i> Eliot, 1903 | Maldiv Islands |
| * <i>Hexabranchnus plicatus</i> Hägg, 1903 | El Tûr, Egypt (Red Sea) |
| <i>Hexabranchnus marginatus</i> var. <i>moebii</i> Eliot, 1905 | Zanzibar |
| <i>Hexabranchnus punctatus</i> Bergh, 1905 | West of Sulawesi, Indonesia |
| * <i>Hexabranchnus aureomarginatus</i> Ostergaard, 1955 | Waikiki, Hawaii |
| * <i>Hexabranchnus tinkeri</i> Ostergaard, 1955 | Waikiki, Hawaii |

considered that *H. sanguineus* was the oldest available name for this species. Currently, this name is used widely as the valid name for the tropical Indo-Pacific species of the genus. Whether *H. morsomus* is the same species is an open question.

In the present study, I attempt to determine how many valid species of *Hexabranchnus* there are, based on the study of specimens collected from the extreme boundaries of the geographic range of the genus. The material examined is deposited at the following institutions: Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, USA (CASIZ), Instituto Nacional de Biodiversidad, Costa Rica (INBio), Natural History Museum of Los Angeles County, USA (LACM), Muséum National d'Histoire Naturelle, Paris, France (MNHN), Marine Invertebrate Museum, University of Miami, USA (UMML) and Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (MNH).

Systematics

Family **HEXABRANCHIDAE** Bergh, 1891

Genus *Hexabranchnus* Ehrenberg, 1831

Hexabranchnus Ehrenberg, 1828–31 [1831]: [30]. Type species (by subsequent designation of J. E. Gray, 1847): *Hexabranchnus praetextus* Ehrenberg, 1828.

Diagnosis

Dorsum smooth, lacking tubercles. Head with two large, flattened and lobate oral tentacles. Anterior border of the foot simple. Gill contractile, not retractile. Radula composed of simple, hamate teeth. Labial cuticle completely covered with rodlets. Buccal mass with numerous and strong muscles attached. Penis and vagina devoid of hooks. Vestibular or accessory glands absent.

Remarks

The genus *Hexabranchnus* has been traditionally placed within the cryptobranch dorids, despite the fact that it lacks the major synapomorphy of this clade, which is the ability to retract the gill into the gill pocket.

Fischer (1880–1887) introduced the taxon Cryptobranchia and included *Hexabranchnus* as one of its three members. Subsequently, Bergh (1891) placed *Hexabranchnus* in its own family, also within the cryptobranch dorids. These opinions were later sustained in the classifications by Odhner in Franc (1968), Thompson (1976) and Rudman (1998). More recently, Wägele and Willan (2000) showed that *Hexabranchnus* is the sister taxon to cryptobranch dorids, but at the same time, they excluded this genus from the Cryptobranchia on the basis of the absence of a retractable gill.

Further phylogenetic studies are necessary to resolve the systematic position of *Hexabranchnus*, which appears to be a derived phanerobranch rather than a cryptobranch dorid (Wägele and Willan 2000).

Hexabranchnus sanguineus (Rüppell & Leuckart, 1830)

(Figs 1A,C, 2–4)

Doris lacera Cuvier, 1804: 452, 453–465, 473, pl. 73, figs 1–3 (*nomen oblitum*).

Doris sanguinea Rüppell & Leuckart, 1828–30: 28–29, pl. 8, fig. 1 (*nomen protectum*).

(For a complete list of synonyms, see Table 1).

Material examined

Syntypes. *Doris lacera* Cuvier. Indian Ocean (= Mer des Indes): date and exact locality unknown, two specimens 30 and 76 mm preserved length, dissected (MNHN).

Syntypes. *Hexabranchnus praetextus* Ehrenberg. Egypt: El Tûr (= Tor), date unknown, one specimen 125 mm preserved length (MNHB 566); El Tûr (= Tor), date unknown, one specimen 110 mm preserved length, partially dissected (MNHB 567).

Other material examined. **Hawaii:** Pono Kai Condominium, Kappa, Kunai Island, 27 Feb. 1986, one specimen 48 mm preserved length, dissected, collected by M. T. Ghiselin (CASIZ 074266). **South Africa:** exact locality unknown, Natal, Nov. 1992, dissected, collected by A. Camnell (CASIZ 087386). **Mozambique Channel:** reef near Hotel Coelacanth, north end of Moroni, Grand Comore Island, 6 Mar. 1975, one specimen 104 mm preserved length, dissected, collected by S. Earle and A. Giddings (CASIZ 068296). **Madagascar:** Tire Reef, 2 km north of Mora Mora Village, 9 Apr. 1989, two specimens 94–100 mm preserved length, dissected, collected by T. M. Gosliner (CASIZ 071897). **Philippines:** Fishery Station Ground, Zamboanga City, Oct. 1947, one specimen 110 mm preserved length, collected by J. S. Domantay (LACM 140743).

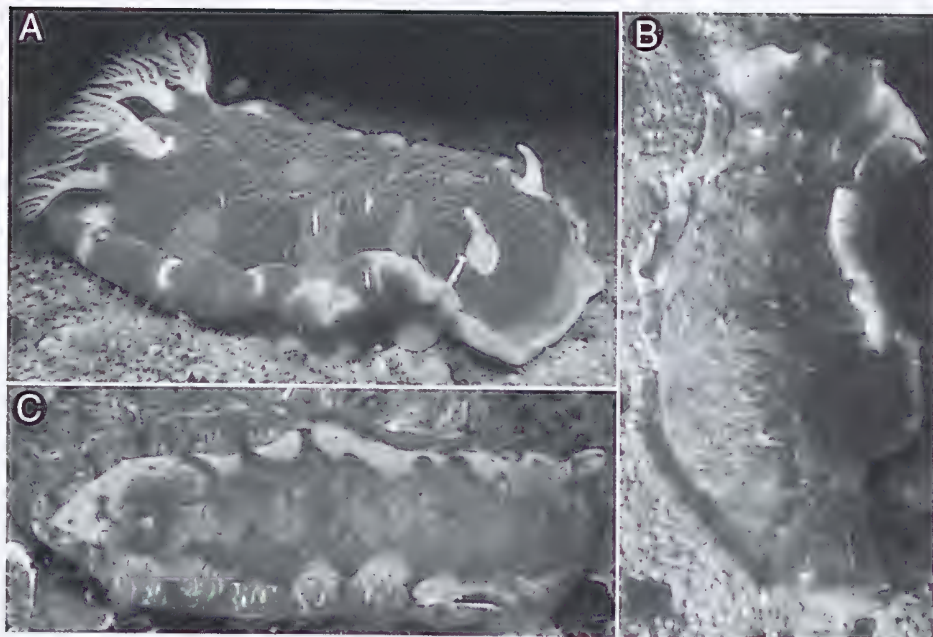


Fig. 1. Living animals. A, *Hexabranhus sanguineus* (Rüppell & Leuckart, 1830) from Indonesia, photograph by M. J. Adams. B, *Hexabranhus morsomus* Marcus & Marcus, 1962 from Panama, photograph by H. Bertsch. C, *Hexabranhus sanguineus* (Rüppell & Leuckart, 1830) from the Philippines, photograph by A. Valdés.

External morphology

The general colour of the living animals is highly variable, from pale orange to bright red (Fig. 1A). In some specimens, there are a number of small white or yellowish dots on some areas or on the entire dorsum (Fig. 1C). Other specimens have large bright red or pinkish spots, or a pale concentric band. Sometimes, the mantle margin is surrounded by a white or yellow line. In other specimens, there is a white area on the inner side of the mantle margin that is visible when the animal is swimming. The rhinophores are red to yellowish, with white spots in some specimens. The gill has normally the same colour as the dorsum, with the rachises of the branchial leaves white or yellowish. The dorsum is smooth. There are seven to nine tripinnate, non-retractile branchial leaves. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 45 lamellae in a 100-mm preserved length specimen.

Ventrally, there are two large, flattened and lobate oral tentacles (Fig. 2B). The anterior border of the foot is simple, lacking a notch and a groove.

Anatomy

The radular formula is $33 \times 49.0.49$ in a 32-mm preserved length specimen (CASIZ 087386), $35 \times 48.0.48$ in a 48-mm preserved length specimen (CASIZ 074266) and $36 \times 77.0.77$ in a 100-mm preserved length specimen (CASIZ 071897). There are no rachidian teeth in any of the specimens examined. The innermost lateral teeth are hamate, with a long apical prolongation and a short, curved cusp (Figs 3A, 4A). In some rows, there is an additional cusp on the outer side of the innermost tooth. The mid-lateral teeth are also

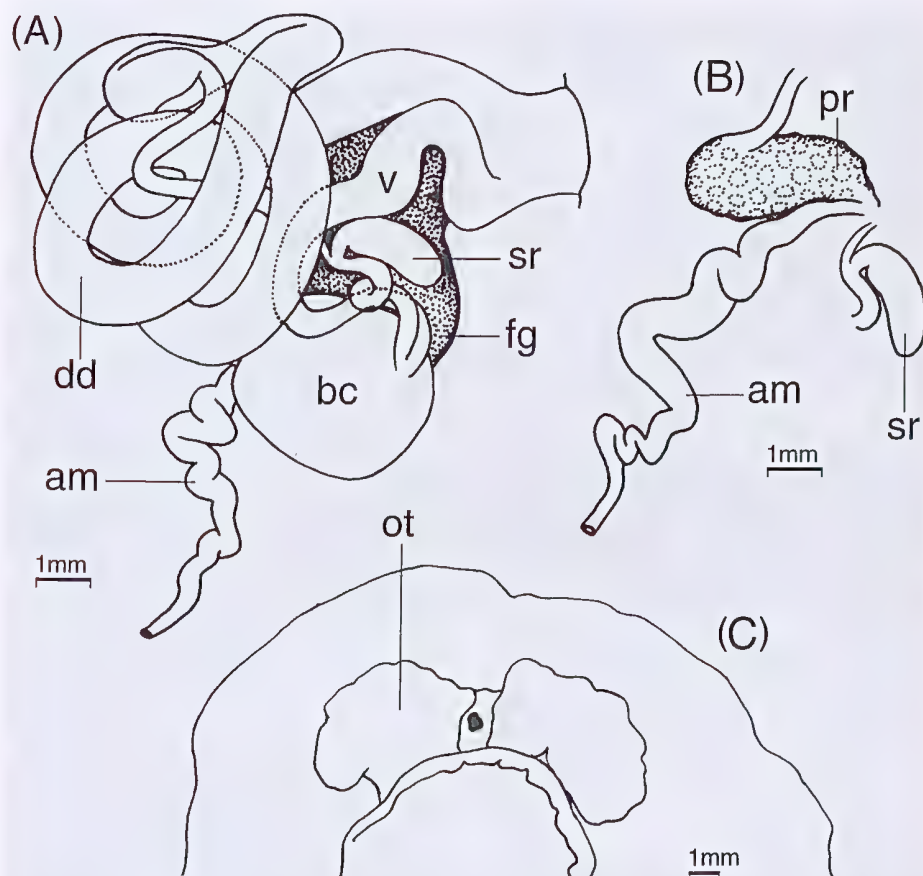


Fig. 2. *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830), anatomy (CASIZ 074266). *A*, Reproductive system. *B*, Detail of several reproductive organs. *C*, Ventral view of the mouth area. am, Ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr, prostate; sr, seminal receptacle; v, vagina.

hamate, but larger and having a longer cusp than the inner laterals (Figs 3*B*, 4*B*). The outermost teeth become smaller again and are similar in shape to the mid-laterals, also having an apical prolongation (Figs 3*C*, 4*C*). The jaws are composed of a number of small and simple rodlets, approximately 30 μ m long (Figs 3*D*, 4*D*).

The reproductive system is triaulic (Fig. 2*A*). The ampulla is very long and convoluted. It branches into the prostatic portion of the deferent duct and the short oviduct that connects to the female glands. The deferent duct is very long and convoluted. The prostatic portion occupies the most proximal end of the deferent duct and is short and glandular; it connects to a short, thin duct that expands into the long, wide, muscular and convoluted ejaculatory portion of the deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is devoid of hooks. The vagina is also wide, long and convoluted. At its proximal end, the vagina connects to the rounded bursa copulatrix. From the bursa copulatrix leads another duct that connects to the beam-shaped seminal receptacle and the female glands.

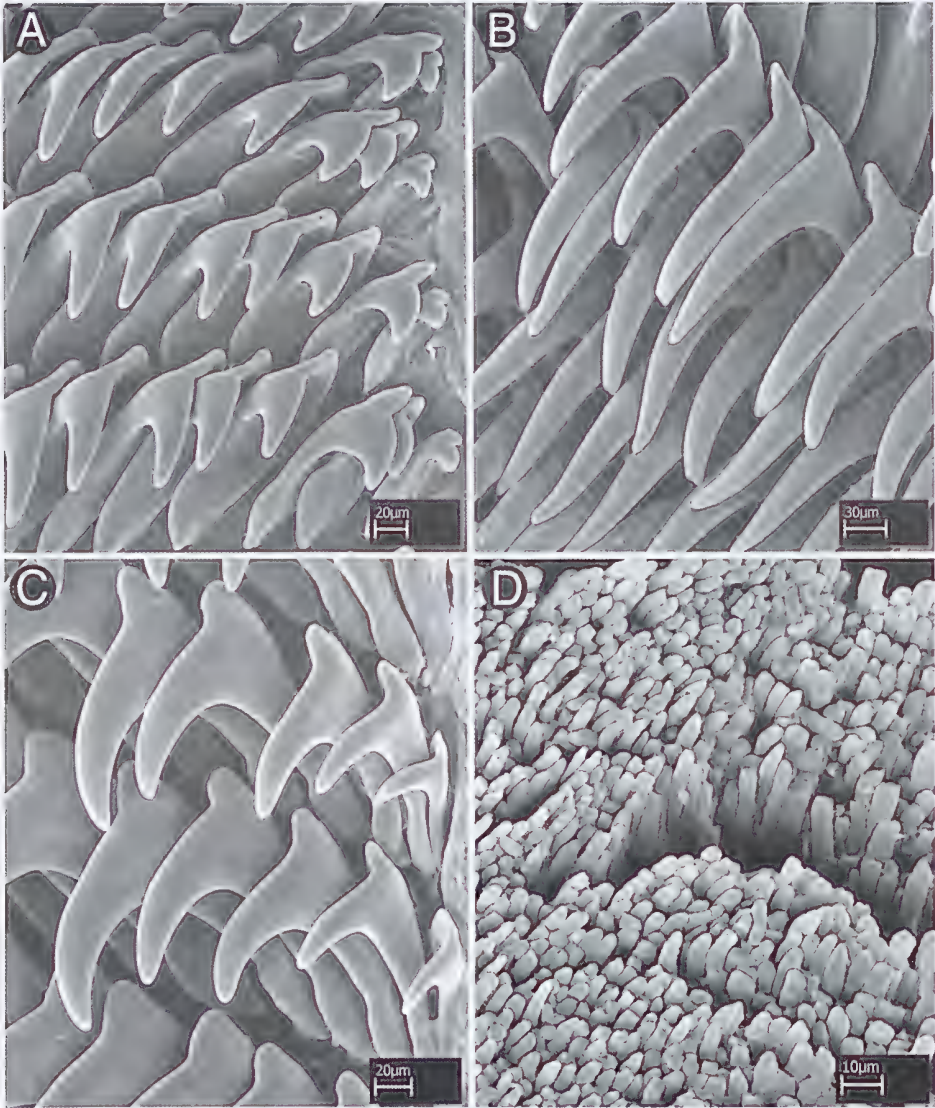


Fig. 3. *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830); scanning electron micrographs of a specimen from South Africa (CASIZ 087386). *A*, Inner lateral teeth. *B*, Lateral teeth from the central portion of the half-row. *C*, Outermost lateral teeth. *D*, Jaw elements.

Geographic range

There are numerous references to this species throughout the tropical Indo-Pacific, from East Africa and the Red Sea to Hawaii (Thompson 1972).

Remarks

Comparison between tropical Indo-Pacific specimens of *Hexabranchnus*, collected from the two opposite boundaries of its geographic range (East Africa and Hawaii) and other localities, confirms that there are no consistent morphological or anatomical differences

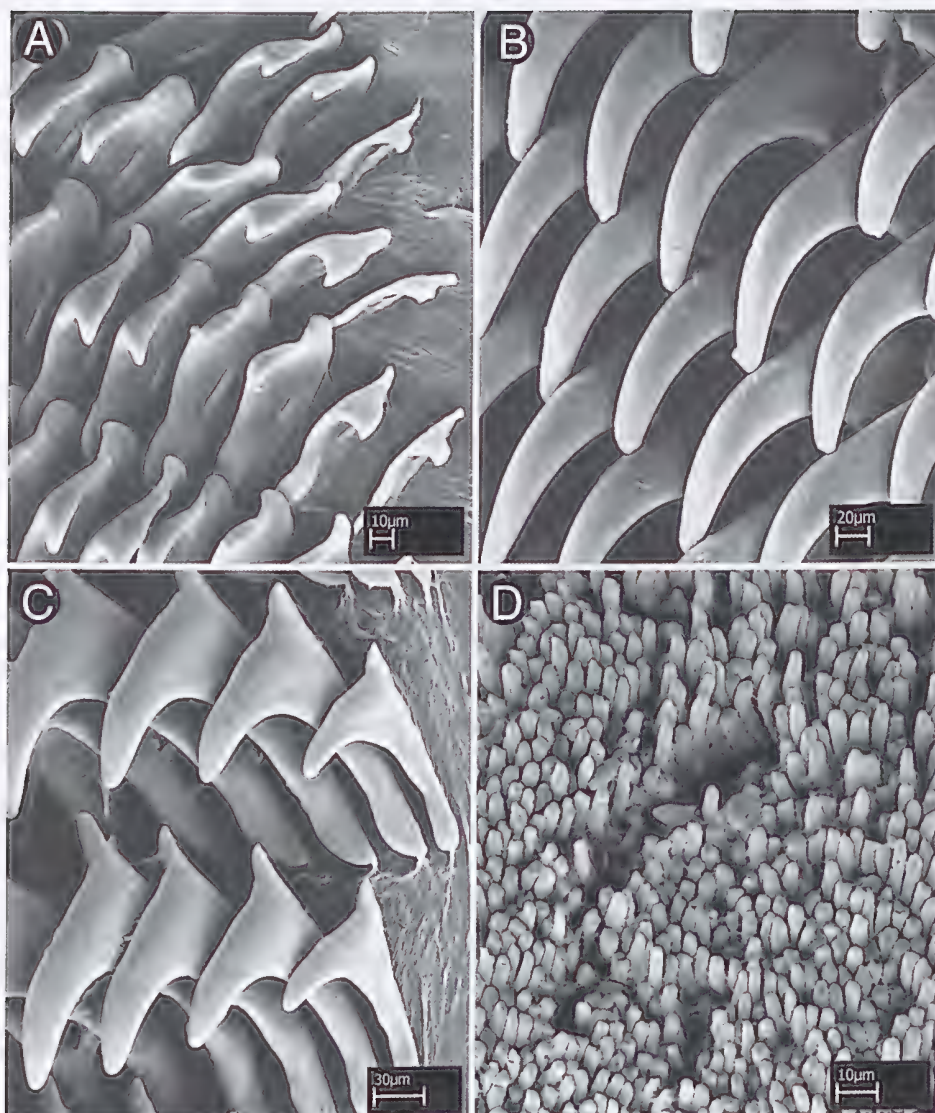


Fig. 4. *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1830); scanning electron micrographs of a specimen from Hawaii (CASIZ 074266). A, Inner lateral teeth. B, Lateral teeth from the central portion of the half-row. C, Outermost lateral teeth. D, Jaw elements.

and, therefore, that only one species of *Hexabranchnus* occurs in this region. Similar conclusions had already been attained by Eliot (1910) and Thompson (1972), but never sustained by anatomical studies.

Following Thompson (1972), all modern authors have been using the name *H. sanguineus* for the tropical Indo-Pacific species of this genus. However, examination of the syntypes of *Doris lacera* Cuvier, 1804 confirms that they belong to the same species and that *Hexabranchnus lacera* constitutes a senior synonym of *H. sanguineus*. *Doris lacera* has been ignored by all authors dealing with the *Hexabranchnus* problem. According to the

International Code of Zoological Nomenclature (ICZN 1999), if a senior synonym has not been used as a valid name after 1899 and its junior synonym has been used for the same species in at least 25 papers, published by at least 10 authors in the immediately preceding 50 years and encompassing a span not less than 10 years, the usage of the junior synonym must be maintained (Article 23.9.1). The name *H. lacer* has only been used as valid in its original description in 1804, whereas the name *H. sanguineus* is in constant usage in modern literature. More than 30 papers, books and field guides using the name *H. sanguineus* as valid have been published during the past 20 years by more than 15 authors. Therefore, the name *H. sanguineus* is here conserved (*nomen protectum*) and *H. lacer* is regarded as invalid (*nomen oblitum*).

According to Winckworth (1941), the original description of *H. sanguineus* and some other species of nudibranchs (see Rüppell and Leuckart 1828–1830; pp. 23–47) was most likely published in 1830. Another synonym of *H. sanguineus*, namely *Hexabranchnus praetextus*, was first and validly introduced in a plate published in 1828, but the written description of the species appeared in 1831 (Winckworth 1941). Again, the name *H. praetextus* has only been used as valid in its original description in 1828–1831. Therefore, the name *H. sanguineus* is here conserved (*nomen protectum*) and *H. praetextus* is regarded as invalid (*nomen oblitum*).

Recently, Johnson (2001) posted photographs of *Hexabranchnus* specimens from Hawaii, which show remarkable colour differences with other specimens of *H. sanguineus* from Hawaii and other Indo-Pacific localities. Johnson (2001) suggested the possibility that the distinct specimens could belong to the species *Hexabranchnus aureomarginatus* Ostergaard, 1955, but anatomical information is required to confirm this. In the meantime, *H. aureomarginatus* is maintained as a synonym of *H. sanguineus*.

Hexabranchnus morsomus Ev. Marcus & Er. Marcus, 1962

(Figs 1B, 5–6)

Hexabranchnus morsomus Marcus & Marcus, 1962: 468–471, figs 16–17.

Material examined

Holotype. British Virgin Islands, Virgin Gorda, Harbour of Spanish Town, 4 Dec. 1959, 26 mm preserved length, dissected, collected by A. Chess (UMML 302696).

Other material examined. **Costa Rica**: Punta Mona (on the west side of the islet), Limón, 19 Oct. 1998, 0 m depth, one specimen 52 mm preserved length, dissected, collected by S. Ávila (INBio 1495908).

External morphology

The general colour of the living animals is orange to reddish, with an irregular pattern of pale orange or yellow pigment. Some specimens have a white powdery colour (Fig. 1B). The mantle margin has a large whitish band situated on the inner end that is only visible when the animal is swimming. The rhinophores are uniformly reddish. The gill is reddish with the apices white. The dorsum is smooth. There are six to seven tripinnate, non-retractile branchial leaves. The anal papilla is prominent, situated in the centre of the branchial circle of leaves. The rhinophores are elongate, having 30 lamellae in a 52-mm preserved length specimen.

Ventrally, there are two large, flattened and lobate oral tentacles (Fig. 5B). The anterior border of the foot is simple, lacking a notch and a groove.

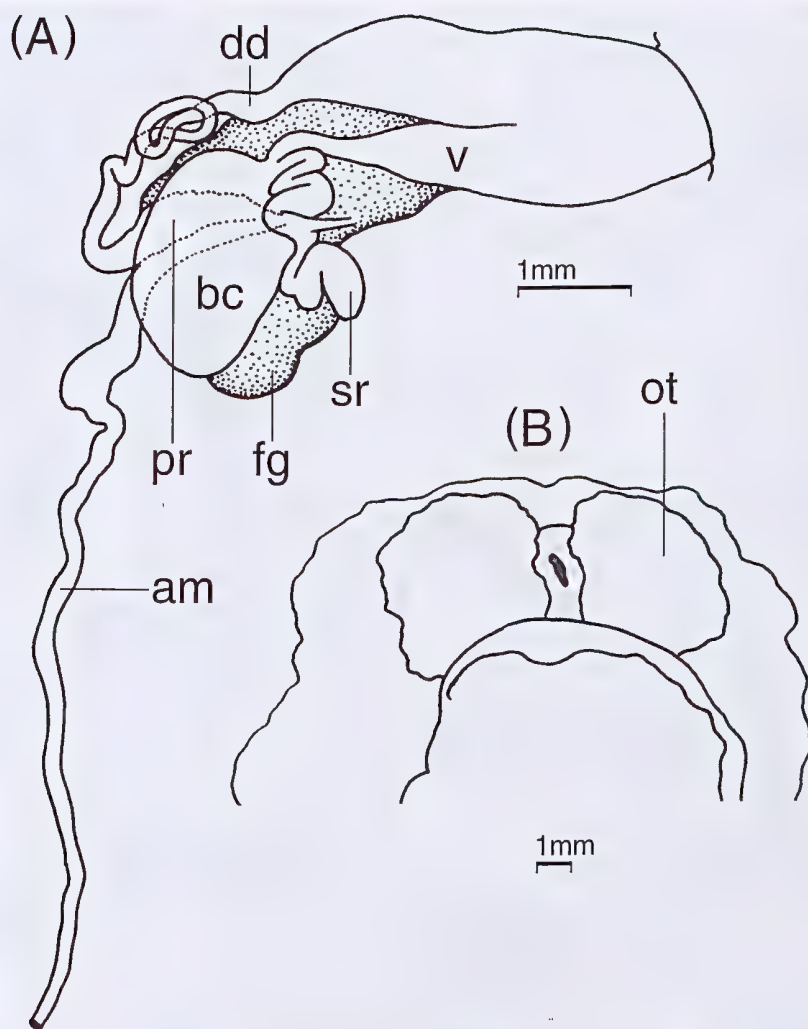


Fig. 5. *Hexabranhus morsomus* Marcus & Marcus, 1962; anatomy (INBio 1495908). A, Reproductive system. B, Ventral view of the mouth area. am, Ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female gland mass; ot, oral tentacle; pr, prostate; sr, seminal receptacle; v, vagina.

Anatomy

The radular formula is $41 \times 116.1.116$ in a 52-mm preserved length specimen (INBio 1495908) and $40 \times 90.1.90$ in a 26-mm preserved length specimen (UMML 302696). There is a small, triangular rachidian tooth in each row. The rachidian teeth have a single, central cusp and a convex base (Fig. 6A). The innermost lateral teeth are hamate, with a small apical prolongation and a short, curved cusp (Fig. 6A). The mid-lateral teeth are also hamate, but larger and have a longer and more straight cusp than the inner laterals (Fig. 6B,C). The outermost teeth become smaller again and are similar in shape to the mid-laterals, having longer apical prolongations and shorter cups (Fig. 6D). The labial cuticle is smooth, devoid of jaws.

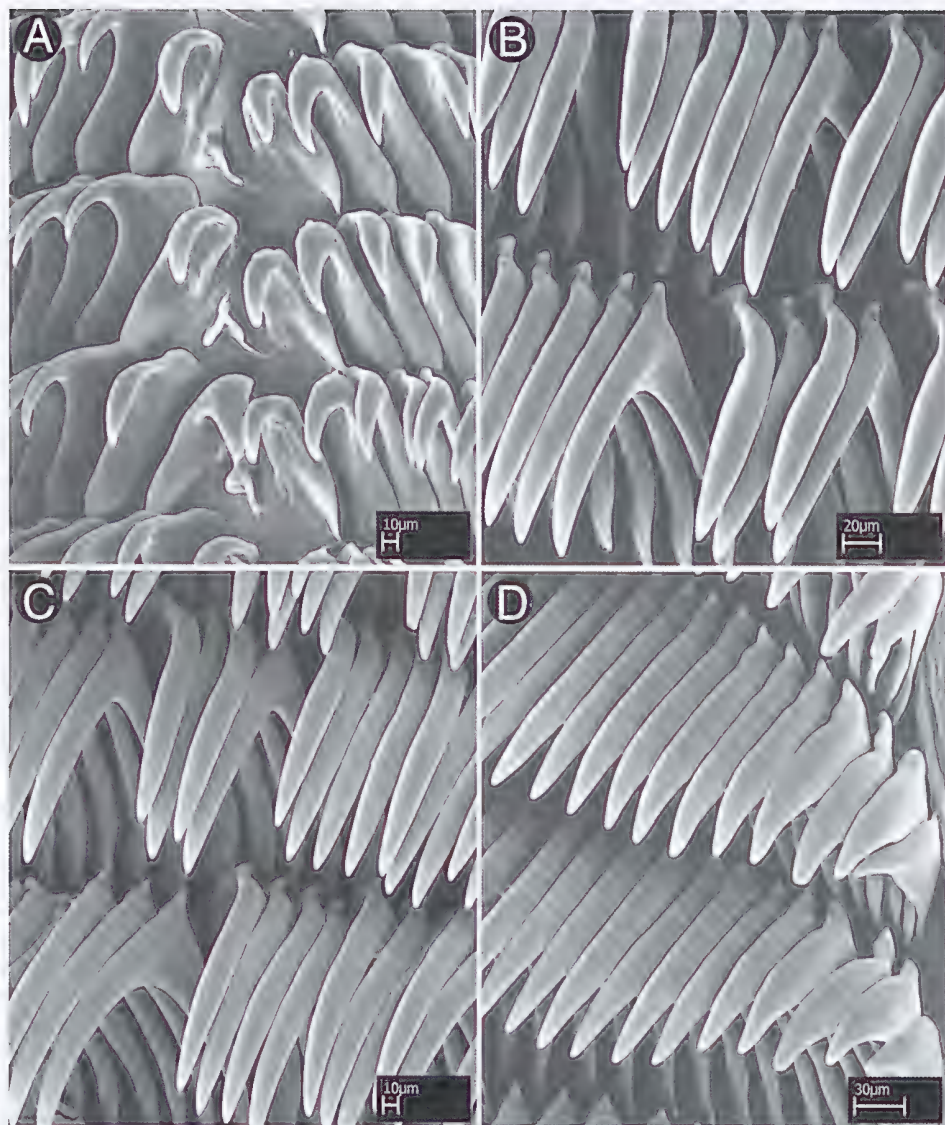


Fig. 6. *Hexabranhus morsomus* Marcus & Marcus, 1962; scanning electron micrographs (INBio 1495908). *A*, Rachidian and inner lateral teeth. *B*, Inner lateral teeth from the central portion of the half-row. *C*, Outer lateral teeth from central portion of half-row. *D*, Outermost lateral teeth.

The reproductive system is triauleic (Fig. 5*A*). The ampulla is very long and convoluted. It branches into the prostatic portion of the deferent duct and a short oviduct that connects to the female glands. The deferent duct is long and convoluted and narrows abruptly at the end of the ejaculatory portion. The prostatic portion occupies the most proximal end of the deferent duct and is short and glandular; it connects to a long, thin and convoluted duct that expands into the wide and muscular ejaculatory portion of the deferent duct. The deferent duct opens into a common atrium with the vagina. The penis is devoid of hooks. The vagina is wide and short. At its proximal end, the vagina connects to the rounded bursa copulatrix.

From the bursa copulatrix leads another duct that connects to the folded seminal receptacle and the female glands.

Geographic range

Only known from the Caribbean Sea, there are records from the British Virgin Islands (Marcus and Marcus 1962), Puerto Rico (Marcus and Marcus 1970), Panama (Meyer 1977) and Costa Rica (present paper).

Remarks

Hexabranchnus morsomus is clearly distinguishable from *H. sanguineus* in several regards. The radulae of the two specimens here studied of *H. morsomus* have rachidian teeth that are absent in all examined specimens of *H. sanguineus*. The inner, mid- and outer lateral teeth of *H. sanguineus* have a long apical prolongation that is absent or very small in *H. morsomus*. The outer teeth of *H. sanguineus* are hook shaped, whereas in *H. morsomus* they are more triangular. It is also remarkable that the labial cuticle of *H. morsomus* is smooth, whereas it is covered with numerous denticles in *H. sanguineus*.

In addition, the reproductive system of these two species is different. The deferent duct and vagina of *H. sanguineus* are very long and convoluted, whereas in *H. morsomus* they are much shorter. Also, the seminal receptacle of *H. sanguineus* is proportionally larger to the bursa copulatrix than that of *H. morsomus* and the duct connecting both organs is shorter in the former species. There is no question that these two species should be maintained separate.

Meyer (1977) considered that *H. morsomus* is most likely a synonym of *H. sanguineus*. She examined five specimens collected from Galeta Point, Panama, and found no rachidian teeth in the radula, except for a few rows in a 20-mm long specimen. Meyer (1977) concluded that this difference probably does not justify, by itself, the separation of two different species. All the specimens examined here of *H. morsomus* have rachidian teeth in all the rows of the radula and also show other consistent differences with specimens of *H. sanguineus* mentioned above. The lack of rachidian teeth in the Panama animals could be due to variability within *H. morsomus* or inaccurate observation (Meyer used a regular compound microscope and, sometimes, rachidian teeth are difficult to observe), but there are enough anatomical differences that justify the maintenance of *H. morsomus* as a valid taxon.

Discussion

The genus *Hexabranchnus* is distributed throughout the tropical Indo-Pacific, from Hawaii to East Africa, and in the Caribbean Sea, but it is absent from other tropical areas in the Eastern tropical Atlantic and the Eastern Pacific. Specimens of *Hexabranchnus* are normally found in shallow coral reef areas (Francis 1980), which are common in the Indo-Pacific and the Caribbean Sea.

There are no published phylogenies on this group that would allow developing a hypothesis about the relationships of *Hexabranchnus* and, therefore, about its origin. However, because there are no more species in this taxon or other dorid nudibranchs with similar anatomical or external features, it can be assumed that *H. sanguineus* and *H. morsomus* are sister taxa. In addition, there are several synapomorphies of *Hexabranchnus*, including the swimming and defensive behaviour (Marcus and Marcus 1962; Edmunds 1968; Bertsch and Johnson 1981), the large and lobate oral tentacles and the smooth dorsum devoid of spicules, that support the monophyly of this taxon.

Assuming that *Hexabranhus* is monophyletic, there are two most likely hypotheses to explain the present distribution of its species. One would involve a split of the original geographic range of the ancestor of these two species and subsequent speciation. In this scenario, the most likely possibility is that the original range of the ancestor was divided during the closure of the Panama land bridge that ended 3.1 million years ago. The absence of *Hexabranhus* species in the Eastern Pacific would be due to subsequent extinction. The vicariant event of the closure of the Panama land bridge has been widely described in the literature for numerous groups of marine animals (Collins 1996), including opisthobranchs (Valdés 2001), and it is considered as a classic example of marine vicariant generalised track (Humphries and Parenti 1986).

The second hypothesis requires that the origin of this genus is situated in either the tropical Indo-Pacific or the Caribbean and that one of these two original populations colonised the other region. This colonisation would have occurred before the closure of the east–west communication. In this scenario, species of *Hexabranhus* probably never became established in the Eastern Pacific or Eastern Atlantic due to the absence of favourable conditions or went extinct subsequently. Accepting any of these hypotheses implies that the two species have been separated for a minimum of 3.1 million years, which would explain the notorious anatomical differences between them.

Acknowledgments

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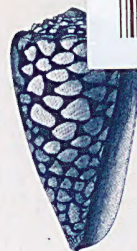
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